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THE GENUS *LYCIANTHES*
(SOLANACEAE) IN
VENEZUELA¹

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ABSTRACT

The 11 species of *Lycianthes* that occur in Venezuela are described and distinguished with illustrations, a dichotomous key, and notes on their appearance and ranges. The separation of *Lycianthes* from *Solanum* and its closer relationship to *Capsicum* are reviewed in light of morphological and recent molecular evidence.

The genus *Lycianthes* (Dunal) Hassl. includes 150–200 species of herbs and shrubs that range throughout the Neotropics and in southeast Asia. A few species have marketable fruits, and one species is sometimes grown as an ornamental, but otherwise the genus is largely unnoticed. This paper reviews characteristics of the genus *Lycianthes* and revises the species that occur in Venezuela. Photographs of some of these plants are presented in Figure 1. Salient features of the flowers of the Venezuelan species are shown in Figure 2.

Lycianthes was long included in the large genus *Solanum*, which is similar in its flowers and fruits and also in its poricidal anthers. *Solanum lycioides* L., a species with seeds enclosed in sclerenchyma,

was separated as the genus *Lycianthes* by Hassler in 1917. Soon after, *Lycianthes* was monographed by Georg Bitter (1920) who expanded the genus to over 100 species, including many lacking sclerenchyma in the fruit. Acceptance of the genus has been hesitant, but most botanists now recognize it as distinct from *Solanum*. D'Arcy (1986) studied the calyx in *Lycianthes*, *Capsicum*, and other relatives and concluded that the unusual calyx warrants generic recognition. He supported Bitter's view that *Lycianthes* is more closely related to *Capsicum* than to *Solanum*. This was accepted by Barboza and Hunziker (1992), Dean (1995), and others. More recently, a classification of the Solanaceae based on chloroplast DNA (Olmstead et al., in press) has

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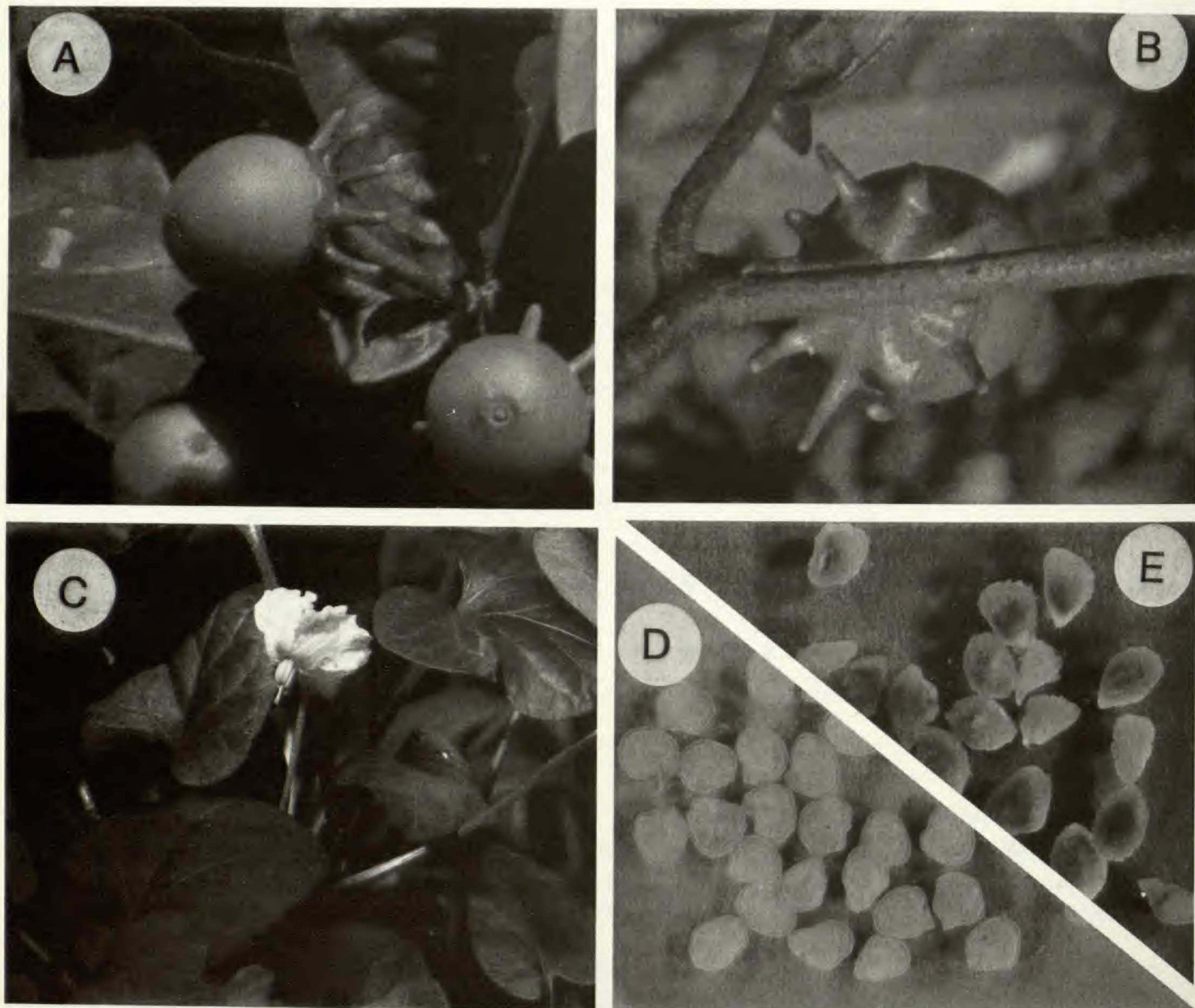


Figure 1. Selected *Lycianthes* species. A, B. *Lycianthes pauciflora*.—A. Fruits and calyx.—B. Fruiting calyx.—C. *Lycianthes asarifolia*. Flowers and foliage.—D. *Lycianthes pauciflora*. Seeds.—E. *Lycianthes lycioides*. Pyrenes. A, B. After Benítez & D'Arcy 3271 (MO, MY). C. After D'Arcy 16261 (MO). D. After Benítez et al. 5148 (MY). E. After Nee 17760 (MO).

supported the separation of *Lycianthes* from *Solanum* and placed it near *Capsicum*.

STONE CELLS

Some solanaceous fruits contain sclerenchyma in the form of stone cells or sclerocytes, which commonly do not enclose the seed. These are aggregates of secondarily hardened parenchyma cells or sclereids. Bitter (1911, 1914) examined many Solanaceae, and he found them in various berries of *Lycianthes*, *Solanum*, and other genera of subfamily Solanoideae. He hypothesized that they might be relics from hard walls of ancestrally capsular fruits. Danert (1969) used electron microscopy to examine their genesis in *Solanum*. Stone cells have been used in the Solanaceae as taxonomic clues (Schilling, 1981), but there is still poor confirmation of their constancy in taxa of different levels. They may be diagnostic in some *Lycianthes* taxa, notably *L.*

lycioides, but are variable in others, such as *L. pauciflora*. Their presence or absence was noted by Bitter, Barboza and Hunziker (1992), and Dean (1995) in their species descriptions.

THE CALYX

In bud, the calyx in *Lycianthes* and *Capsicum* is fused to the top (complete prefloration), and the corolla, stamens, and other interior parts egress from it by a stretching of the calyx apex. This results in a truncate margin subtended by a thin sleeve of tissue with reduced vasculature. Low in the calyx, the five principal calyx traces each diverge into three traces, much as in a foliage leaf, and the adjacent lateral traces are fused together, resulting in a calyx with 10 nerves. Of these, 5 primary ones are produced by the continuation of the principal calyx traces, and 5 are produced secondarily by fusion of the adjacent lateral traces. In

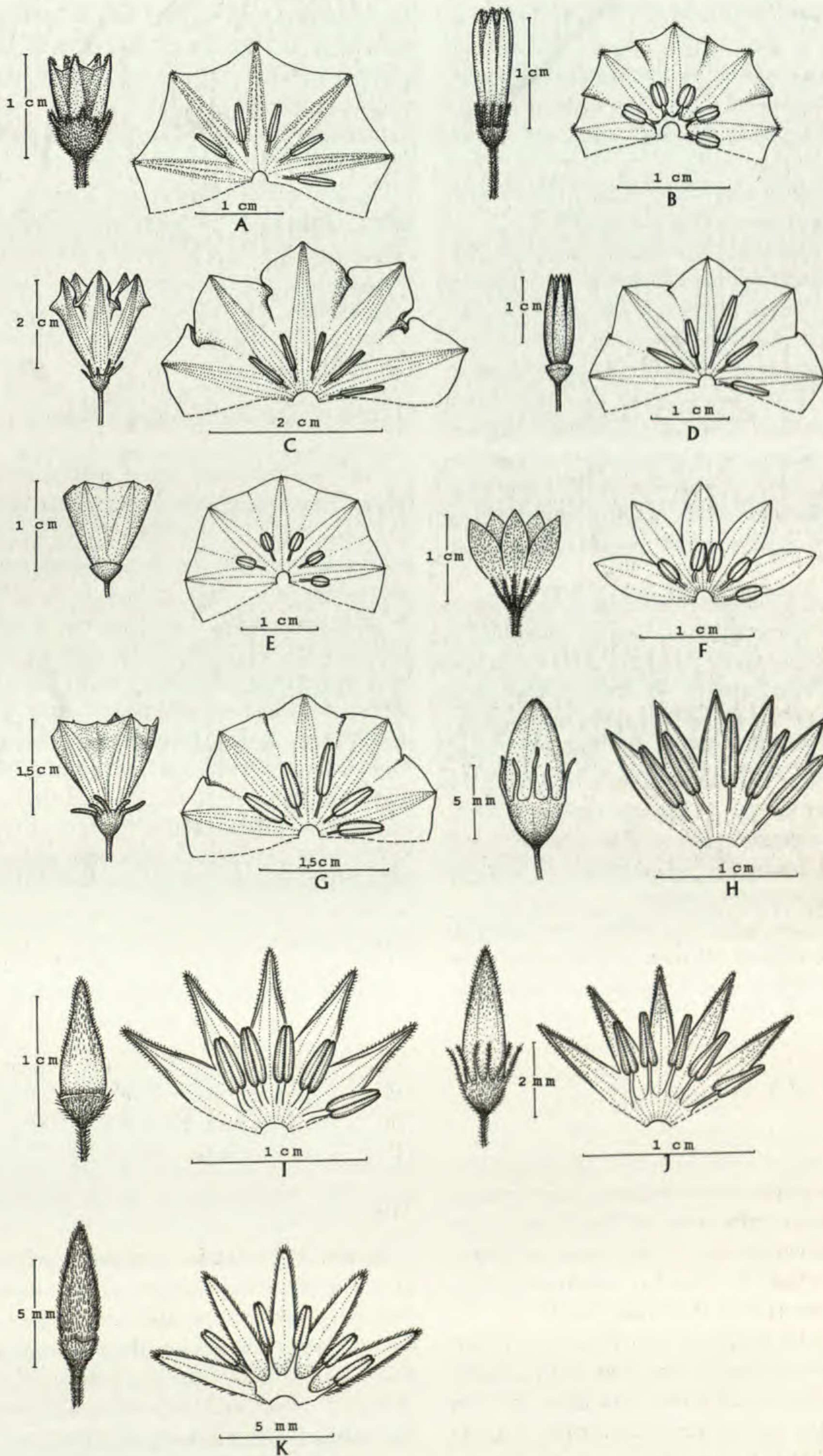


Figure 2. Closed and open flowers of Venezuelan species of *Lycianthes*. Left figure: closed floral buds showing the calyx. Right figure: open flower showing corolla lobing and relative size of stamens.—A. *Lycianthes ferruginea*.—B. *Lycianthes lycioides*.—C. *Lycianthes lenta*.—D. *Lycianthes sanctaemarthae*.—E. *Lycianthes asarifolia*.—F. *Lycianthes acutifolia*.—G. *Lycianthes pauciflora*.—H. *Lycianthes stenoloba*.—I. *Lycianthes inaequilatera*.—J. *Lycianthes amatitlanensis*.—K. *Lycianthes radiata*. A. After Morillo 6057 (VEN); B. After Ruíz-Terán 12533 (MY); C. After Bunting 4433 (MY); D. After Steyermark 122959 (MO); E. After Liesner et al. 7803 (VEN); F. After Ruíz-Terán 64 (MERF); G. After Ferrari 733 (MY); H. After Mocquerys 978 (VEN); I. After Davidse 18899 (VEN); J. After Steyermark 121528 (VEN); K. After Steyermark 56628 (MY).

many cases, some or all of these 10 traces enate or bend outward to form umbos or teeth laterally on side of the calyx and below the apical sleeve area. Thus, in *Lycianthes* calyces, all teeth or umbos are lateral and arise below the calyx apex, and no primary teeth are found at the top of the calyx. These structures are shown in Figure 2, and their vasculature was illustrated by D'Arcy (1986).

The extent of lateral vein enation is variable, differing in different species, sometimes in different flowers on the same plant, and sometimes in different veins on the same flower. In different species, there may be no teeth at all or any number from 1 to 10. When there are 10 teeth, they often form two series, the 5 teeth arising from the primary traces larger than those arising from the fused lateral traces. In *Solanum*, calyces have as many teeth as corolla lobes or stamens, usually 5, rarely 4 or 6. Having 4–6 calyx teeth is quite unusual in *Lycianthes*.

The calyx in *Lycianthes*, thus, has three features, thought to be specializations, that are not found in the calyx of *Solanum*: (1) complete prefloration and egress of interior parts by stretching rather than bending out and tearing, which produces an entire, thinned, apical sleeve; (2) fused adjacent lateral traces of the ancestral lobes; and (3) enation of the traces in many species to produce umbos or teeth. However, because they are so alike in other ways, *Solanum* and *Lycianthes* are assumed to be derived from a closely related ancestor.

Whether *Solanum* and *Lycianthes* arose independently from a common ancestor or *Lycianthes* arose from within *Solanum* is not revealed in morphological studies of the calyx. The trees used by Olmstead et al. (in press) to illustrate their classification of the Solanaceae depict one clade leading to two phylads (*Lycianthes/Capsicum* and *Solanum/Jaltomata*), each with taxa displaying both porose and longitudinal anther dehiscence. All the porose-dehiscent Solanaceae except the enigmatic *Triguera* of Gibraltar and nearby areas are thus contained in this single clade, and the question remains whether porose dehiscence was derived twice within the clade or was derived once and lost twice.

In *Capsicum*, although calyx prefloration is complete and egress of the interior parts is by stretching as in *Lycianthes*, the sleeve is smaller and less evident, and the lateral traces do not fuse and do not enate to produce secondary umbos or teeth. Thus, *Capsicum* has only two of the three specializations noted above for *Lycianthes*: the complete prefloration and stretching egress of the floral parts, and the enation of primary traces to produce teeth. The fusion of adjacent lateral veins and enation of

a second series of teeth is hardly indicated or not present at all. *Capsicum* calyces have 5 teeth; *Lycianthes* calyces seldom have 5 teeth, they usually develop either 10 teeth or fewer than 5.

In his morphological study, D'Arcy (1986) suggested that floral parts in *Witheringia* have a basically similar way of egressing from the calyx and that this genus is probably closely related to the *Lycianthes/Capsicum* group, but the recent study of Olmstead et al. (in press) gives a more distant placement.

OTHER CHARACTERS

Other characters are also useful for recognizing *Lycianthes*, although they are not diagnostic. Leaves are always simple and entire, most anthers are yellow or orange, and, with the exception of *Lycianthes lycioides*, seeds are discoid with the embryo coiled around the edge of the seed and surrounding the endosperm as is usual in seeds of the Solanoideae. In most species (all those found in Venezuela), inflorescences are fascicles or solitary flowers and lack peduncles; anthers open by small terminal pores, corollas are rotate, and the fruit is an orange or red berry. Seeds are numerous, except in *L. lycioides*. In most characters, plants of *Lycianthes* are much like those of related genera such as *Solanum*, *Physalis*, and *Capsicum*.

Diversity of corolla shape and androecium appearance is shown in Figure 2.

HAIR TYPES

Several hair types, simple, branched, and stellate, are found in the indumentum of Venezuelan species of *Lycianthes*, and these tend to have taxonomic correlation and diagnostic value at the sectional level. In the Venezuelan species, all hairs are uniseriate, and glandular hairs are not found. Simple hairs are usually several cells long with little noticeable differentiation. In section *Simplicipila*, coarse and tawny simple hairs give a strigose appearance. In *Lycianthes acutifolia*, a basal expansion, not unlike that found in many Boraginaceae (pers. obs.), gives the simple hair on the leaf lamina the appearance of arising from a translucent foot. Many species have only simple hairs. Species with branched or stellate hairs often also have simple hairs. Hairs with the radii all arising at one point are termed stellate; when radii arise along the stalk they are referred to as branched (Roe, 1971; Seithe, 1962; Haegi, 1991). On some parts, especially abaxially on the corolla, hairs may be reduced to simpler, difficult-to-interpret types.

Seithe (1962), in her study of hairs in *Solanum*,

examined 25 species of *Lycianthes*. Among these were six that occur in Venezuela: *amatitlanensis*, *asarifolia*, *acutifolia* (*conicibaccata*), *lenta* (*variifolia*), *radiata* (*goudotii*), and *stenoloba* (*stephanocalyx*). She concluded that the elaboration of hair types in *Lycianthes* evolved independently from that in *Solanum*. She hypothesized that in *Lycianthes* stellate hairs arose from branched hairs, unlike in *Solanum* where they arose from gland-tipped hairs. Unfortunately, she did not distinguish between the simple, eglandular hairs (*Fingerhaare*) characteristic of many species of *Solanum* and the coarse, tawny strigose hairs of some *Lycianthes*, which seem quite different in nature. These simple hairs in *Lycianthes* may also be independent in origin from those in *Solanum*.

USES

Fruits of some species, *Lycianthes asarifolia* in Venezuela and elsewhere, are sometimes eaten, and some, *L. moziniana* (Dunal) Bitter and others in Mexico (Williams, 1993; Dean, 1995), even reach fruit markets. *Lycianthes rantonnei* (Carrière) Bitter is grown as an ornamental in upland tropical gardens. No other uses are known.

CHEMISTRY

Lycianthes has a suite of alkaloids comparable to other genera of Solanaceae (Roddick, 1986), but few species have been examined (Bradley et al., 1978; Evans & Somanabandhu, 1980; Lin et al., 1987; Ripperger & Porzel, 1992), none of these species occurring in Venezuela.

SYSTEMATICS OF LYCIANTHES

Lycianthes was divided into a hierarchy of subgenera, sections, and series by Bitter (1920), only some of which are represented in Venezuela. The subgenera and sections in Venezuela are amply distinct and not likely to be confused. Within the sections, however, distinctions are often difficult to make, and species limits are sometimes poorly known. The type species, *Lycianthes lycioides*, has fruits with eight or fewer seeds that are enclosed in sclerenchyma as pyrenes. It constitutes a perhaps monospecific subgenus and section. In the other four sections, seeds are numerous and not enclosed in sclerenchyma. Section *Asaropsis* includes one or perhaps three species of ground creepers. Section *Simplicipila* includes perhaps a dozen species of weak shrubs with strigose hairs. Section *Polymeris* includes many species of night-blooming climbers. Series *Oligochondra* and *Virgatae* are separated by presence or absence of stone cells in the fruit.

Subgenus *Lycianthes* (*L. lycioides*): seeds enclosed as pyrenes.

Section *Lycianthes* (*L. lycioides*): erect, woody shrubs; flowers diurnal; stamens unequal (3+2).

Subgenus *Polymeris* (Dunal) Bitter: seeds numerous, not enclosed in sclerenchyma; fruits sometimes with stone cells.

Section *Asaropsis* Bitter (*L. asarifolia*): plants procumbent; leaves cordiform; flowers solitary, diurnal; stamens equal; stone cells wanting.

Section *Polymeris*: shrubs or climbers; flowers fasciculate, nocturnal; calyx teeth 10 in 2 unequal series; stamens unequal (4+1); stone cells often present.

Series *Oligochondra* Bitter (*L. ferruginea*, *L. pauciflora*, *L. stenoloba*): plants high climbing or erect, small shrubs; flowers fasciculate, nocturnal; fruits dangling, stone cells often present.

Series *Virgatae* Bitter (*L. lenta*, *L. sanctaemarthae*): plants low climbers; flowers fasciculate, nocturnal; fruits dangling, stone cells wanting.

Section *Simplicipila* Bitter (*L. acutifolia*, *L. amatitlanensis*, *L. inaequilatera*, *L. radiata*): subshrubs; flowers fasciculate, diurnal; stamens equal; fruits held erect, stone cells present or not.

GEOGRAPHY OF LYCIANTHES

Lycianthes is confined to the Neotropics and to southeast Asia. Most of the species and most of the diversity is in the New World, with distinctive groups in Mexico and Central America. Section *Lycianthes* (*L. lycioides*) is restricted to South American uplands. Section *Asaropsis* includes one (or two) species that grow in lowlands in eastern South America. *Lycianthes asarifolia*, of this section, was recently reported as introduced into Texas (Darwin & Feibelman, 1991). This section may also embrace *L. lysimachioides* (Wall.) Bitter, a wide-ranging southeast Asian species that has similar growth form and anthers, but which has well-developed teeth on the calyx. Section *Polymeris* and its similar series *Oligochondra* and *Virgatae* are widespread at lower and middle elevations in South and Central America and the Antilles. Section *Simplicipila* has a similar range but is not known from the Antilles, and it may not range north of Nicaragua.

SCOPE OF THE PRESENT STUDY

Both authors have studied plants of *Lycianthes* in various countries for more than two decades, but the present focus that led to this paper dates from

funding from binational grants in 1991. This permitted three extensive field trips to cover almost all parts of Venezuela thought to host *Lycianthes* species, also study of a large suite of borrowed herbarium specimens by both authors at the Missouri Botanical Garden, St. Louis. Many other smaller field trips were made in Venezuela during this period, and other herbaria were visited. Many of the species were grown for observation in the St. Louis greenhouse.

Considering the large range sizes of some species and frequent occurrence in disturbed habitats, the number of specimens in herbaria is disappointingly low (D'Arcy, 1973: 632; Nee, 1981). This has meant few observations and scant data in some cases, leading to hesitancy in assigning species names and in documenting ranges outside of Venezuela. Despite our efforts, the genus remains seriously undercollected in Venezuela, and further work should enhance knowledge of the genus.

LYCIANTHES in Venezuela

In Venezuela we record 11 species of *Lycianthes*. They include procumbent herbs (*L. asarifolia*), erect shrubs (*L. lycioides*), arching subshrubs (*L. amatitlanensis*, *L. inaequilatera*), and climbers that remain in the understory (*L. lenta*) or climb to the canopy (*L. pauciflora*). All are perennial. Some species have diurnal flowers that generally lack scent, while others have fragrant flowers that are open at night. Night scented flowers have been observed to open just before dusk and to close after dawn. Most species are found at low elevations, but some species (*L. ferruginea*, *L. radiata*, *L. acutifolia*) range into cloud forests at upper elevations, and *L. lycioides* is found up to 3500 m elevation. *Lycianthes asarifolia* and *L. lenta* are often adventive in secondary habitats, and the latter, circum-Caribbean in distribution, is often found near the sea.

KEY TO SPECIES OF LYCIANTHES in Venezuela

- 1a. Leaves either basally cordate or conspicuously oblique, minor leaves often present; corollas white, mostly one opening at a time, diurnal; hairs mostly simple; stamens all alike (*Asaropsis*, *Simplicipila*).
 - 2a. Leaves basally cordate, glabrous; plants creeping or procumbent; flowers solitary, deflexed on erect peduncles held erect above the leaves (*Asaropsis*)..... *L. asarifolia*
 - 2b. Leaves conspicuously oblique, pubescent; plants erect; flowers fasciculate, erect on the pedicels but held beneath the leaves (*Simplicipila*).
 - 3a. Calyx teeth wanting (the 10 nerves slightly elevated and often conspicuous, often splitting in fruit to appear tooth-like)..... *L. radiata*
 - 3b. Calyx teeth conspicuous, surpassing the margin of the calyx.
 - 4a. Calyx 2 mm long or longer, calyx teeth 2–3 mm long; berry more than 6 mm long.
 - 5a. Corolla more than 9 mm long; fruiting pedicels mostly more than 15 mm long; fruit oblong to conical (often above 1200 m elevation in Venezuela)..... *L. acutifolia*
 - 5b. Corolla less than 9 mm long; fruiting pedicels less than 15 mm long; fruit globose (not above 1200 m elevation in Venezuela)..... *L. amatitlanensis*
 - 4b. Calyx less than 2 mm long, calyx teeth less than 0.7 mm long; berry 5–6 mm long..... *L. inaequilatera*

TAXONOMIC TREATMENT

Lycianthes (Dunal) Hassl., *Annuaire Conserv. Jard. Bot. Genève* 20: 180. 1917. Based on *Solanum* sect. *Pachystemonum* subsect. *Lycianthes* Dunal, in DC., *Prodr.* 13(1): 29. 1852. *Solanum* series *Meiomeris* Dunal, in DC., *Prodr.* 13(1): 29; 156. 1852. *Solanum* subg. *Lycianthes* (Dunal) Bitter, *Bot. Jahrb. Syst.* 54: 424. 1917. *Otilix* Raf., *Med. fl.* 2: 87. 1830. *Solanum* sect. *Lycianthes* (Dunal) Wettst., in A. Engler & K. Prantl, *Nat. Pflanzenfam.* 4(3b): 22. 1891. TYPE: *Solanum lycioides* L.

Parascopolia Baill., *Hist. pl.* 9: 338. 1888. TYPE: *Parascopolia acapulcensis* Baill. = *Lycianthes acapulcensis* (Baill.) D'Arcy.

The name *Lycianthes* is conserved against *Otilix* Raf. and *Parascopolia* Baill.

Perennial herbs, shrubs, or vines; pubescence of simple or branched hairs. Leaves often geminate, simple, entire, membranous to coriaceous, petiole. Inflorescences mostly solitary flowers or fasciculate at leaf axils. Flowers diurnal or nocturnal, often only a few opening at a time, sometimes showy, mostly 5-merous; calyx cupular, apically truncate, 10-nerved, the nerves often enated into lateral teeth, pubescent or glabrous; corolla white, blue, or purplish, mostly rotate or reflexed, apically subentire or deeply divided; stamens equal or not, anthers yellow (the Venezuelan species), held together in a cone, rarely connate, the pores mostly minute and terminal, rarely elongate, adaxial slits; ovary spherical or conical, style slender, mostly glabrous, stigma capitate, sometimes bilobate; ovules many. Fruit a fleshy or juicy berry, mostly red, orange, or yellow, usually globose or nearly so, stone cells (sclerocytes) present in some species; seeds many, mostly discoid, light colored, testa reticulate; embryo coiled around the periphery of the testa.

- 1b. Leaves basally narrowed or truncate, often symmetrical, minor leaves seldom present; corollas white, blue, or violet, several opening at a time, often crepuscular or nocturnal; hairs mostly branched or stellate; stamens unequal (*Lycianthes*, *Polymeris*).
- 6a. Plants erect, branches rigid, sometimes with spinose branches; leaves small (less than 1 cm wide); stamens with 3 longer and 2 shorter filaments; fruit less than 6 mm across; seeds fewer than 8, enclosed in sclerenchyma as pyrenes (*Lycianthes*) *L. lycioides*
 - 6b. Plants generally climbing, branches flexuous, often sprawling, unarmed; leaves large (more than 1.5 cm wide); stamens with 1 longer and 4 shorter filaments; fruits more than 6 mm across; seeds mostly more than 8, the testa entirely visible, not enclosed in sclerenchyma (*Polymeris*).
 - 7a. Calyx lacking teeth..... *L. sanctaemarthae*
 - 7b. Calyx with conspicuous teeth.
 - 8a. Pubescence of simple hairs; calyx teeth in one series; corolla lobed; fruiting calyx teeth ascending or spreading, almost as long as the fruit..... *L. stenoloba*
 - 8b. Pubescence of branched or stellate hairs; calyx teeth in two series; corolla subentire or lobed; fruiting calyx teeth reflexed or spreading, much shorter than the fruit.
 - 9a. Leaves evenly puberulent overall with minute stellate hairs, leaf bases mostly truncate or rounded, leaves near the inflorescences mostly less than 4 cm long; fruits less than 9 mm across, lacking stone cells..... *L. lenta*
 - 9b. Leaves glabrate with scattered coarse stellate hairs, leaf bases mostly obtuse or cuneate, pointed, leaves commonly more than 5 cm long; fruits more than 10 mm across, mostly with stone cells.
 - 10a. Plants copiously pubescent with yellowish or reddish brown hairs, the pedicels tomentose, corolla lobes greenish and the folds white; found between 1200 and 2900 m in Venezuela... *L. ferruginea*
 - 10b. Plants glabrescent, pedicels glabrate, corolla mostly uniform yellow; found between 600 and 1500 m in Venezuela..... *L. pauciflora*

CLAVE DE LAS ESPECIES DE LYCIANTHES DE VENEZUELA

- 1a. Hojas basalmente cordadas u oblicuas; hojas menores generalmente presentes; corolas blancas, abriendo una flor por inflorescencia, diurnas; estambres iguales; tricomas generalmente simples (*Asaropsis*, *Simplicipila*).
 - 2a. Plantas rastreras o procumbentes, glabras, flores solitarias, colgantes sobre pedúnculos erectos y colocadas arriba de las hojas (*Asaropsis*)..... *L. asarifolia*
 - 2b. Plantas erguidas no enraizando en los nudos, pubescentes, flores fasciculadas, erectas, colocadas debajo de las hojas (*Simplicipila*).
 - 3a. Cáliz sin dientes, los 10 nervios conspicuos y un tanto elevados..... *L. radiata*
 - 3b. Cáliz con dientes conspicuos excediendo el margen del cáliz.
 - 4a. Dientes del cáliz iguales o mayores de 2 mm de longitud; frutos mayores de 6 mm de longitud.
 - 5a. Corola igual o mayor de 9 mm de longitud; frutos oblongos, cónicos u ovoides; pedicelos fructíferos mayores de 15 mm de longitud; localizada encima de 1500 m de elevación en Venezuela..... *L. acutifolia*
 - 5b. Corola menor de 9 mm de longitud; frutos globosos; pedicelos fructíferos menores de 15 mm de largo; localizada debajo de 1200 m de elevación en Venezuela..... *L. amatulanensis*
 - 4b. Dientes del cáliz menores de 0.7 mm de longitud; frutos 5–6 mm de longitud..... *L. inaequilatera*
- 1b. Hojas basalmente truncas o angostas, con frecuencia simétricas; hojas menores rara vez presentes; corolas blancas, azules o violeta, abriendo varias por inflorescencia, con frecuencia crepusculares o nocturnas; estambres desiguales; tricomas generalmente estrellados o ramificados (*Lycianthes*, *Polymeris*).
 - 6a. Plantas erguidas con ramas espinescentes, tricomas ramificados, hojas pequeñas (menos de 1 cm de ancho); frutos menores de 6 mm de diám., semillas menos de 8, incluídas en pirenos (*Lycianthes*)..... *L. lycioides*
 - 6b. Plantas generalmente trepadoras o cuando erguidas con ramas apoyantes, inermes, pelos estrellados o simples, hojas grandes (mas de 1.5 cm de ancho); frutos mayores de 6 mm diám., semillas mas que 8, no incluídas en pirenos (*Polymeris*).
 - 7a. Cáliz edentado..... *L. sanctaemarthae*
 - 7b. Cáliz con dientes subapicales conspicuos.
 - 8a. Plantas con tricomas simples; dientes del cáliz en una serie; corola con el borde lobado; en fruto, los dientes del caliz erguidos y casi tan largos como el fruto..... *L. stenoloba*

- 8b. Plantas con tricomas estrelladas o ramificadas; dientes del cáliz en dos series desiguales; corola con el borde casi entero o lobado; en fruto, los dientes del caliz extendidos o reflejos y menores que el fruto.
- 9a. Plantas en conjunto pubescentes con pelos estrellados diminutos, hojas basalmente truncas o redondas, hojas cercanas de las inflorescencias generalmente menor de 4 cm de largo; fruto menor de 9 mm de ancho, sin células pétreas..... *L. lenta*
- 9b. Plantas glabrescentes y con escasos pelos estrellados o tomentosas, hojas basalmente obtusas o cuneadas, hojas generalmente mayores de 5 cm de largo; fruto mayor de 10 mm de ancho, con frecuencia con células pétreas.
- 10a. Plantas pubescentes, pedicelos tomentosos; corola con los lobos verdes y el pliegue blanco; localizadas en elevacionales entre 1200 y 2900 m..... *L. ferruginea*
- 10b. Plantas glabrescentes, pedicelos glabros; corola generalmente con coloración uniforme; localizadas en elevacionales entre 600 y 1500 m..... *L. pauciflora*

1. *Lycianthes acutifolia* (Ruiz & Pav.) Bitter, Abh. Naturwiss. Vereine Bremen 24 (1): 453. 1919 [1920]. *Solanum acutifolium* Ruiz & Pav., Fl. peruv. 2: 33, t. 162, fig. b. 1799. TYPE: Peru. Muña, Ruiz s.n. (B destroyed, = F photo 2561).

Lycianthes xylopiifolia (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 454. 1919 [1920]. *Solanum xylopiæfolium* Dunal, in DC., Prodr. 13(1): 179. 1852. TYPE: Venezuela. Colonia Tovar, Moritz 825 (holotype, G-DC, = F photo 6765).

Lycianthes goudotii var. *uberior* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 436. 1919 [1920]. *Lycianthes conicibaccata* Bitter ex Seithe, Bot. Jahrb. Syst. 81: 313. 1962. TYPE: Colombia. Chiquiniquita, Boyacá (Bogotá fide Seithe), blühend July 1909, Frère Félix s.n. (holotype, M not seen).

Lycianthes xylopiifolia var. *intermedia* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 455. 1919 [1920]. SYNTYPES: Venezuela. Colonia Tovar, Moritz 345 (BM not seen); Fendler 974 (G not seen, MO, P).

Lycianthes xylopiifolia var. *maxima* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 455. 1919 [1920]. TYPE: Venezuela. Colonia Tovar, Gollmer s.n. (holotype, B not seen).

Lycianthes lehmannii Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 444. 1919 [1920]. TYPE: Colombia. Alto de Cuitambo, Vulkan Sotarâ, Lehmann (B not seen, = F photo 2581).

Erect *subshrub* 0.5–2 m high, branches weak, slender, drying brown, sometimes dark or reddish, sparingly ascending-strigose; pubescence of coarse tawny hairs, the bases often expanded and foot-like. *Leaves* unequal-geminate, ovate, mostly narrow, sometimes oblique, 5–7 × 1.5–6 cm, membranous, above sometimes slightly bullate, paler beneath, veins 6–8 on each side, plane or slightly impressed above, elevated beneath, with scattered hairs above, mostly sparingly glabrescent; petioles 3–15 mm long; minor leaves obovate, 1–3 × 1–2 cm, sessile or short-petiolate. *Inflorescences* solitary flowers in leaf axils. Flowers downward-directed;

pedicels 1–2.3 cm long, pubescent; *calyx* 2–4 × 3–5 mm, the cup densely strigose, teeth 10 in one series, 2–3(–6) mm long, weak, erect at anthesis, pubescent; corolla white, 8–15 mm × 1–3 cm, lobed ½–⅓ way down, the lobes spreading or recurved, pubescent outside, especially distally; stamens unequal, 4 filaments 1.5–2.5 mm long, 1 filament 2–3 mm long, anthers 2–3 mm long; ovary subglobose to conical, 1–2 × 0.5–1 mm, style 7–7.5 mm long, exerted 2.5 mm, stigma subglobose. *Berry* yellow to orange, conical, ovoid, or oblong, 6–13 × 4–12 mm, stone cells lacking; fruiting calyx 4–5 mm long, applied to the berry, pubescent, the slender teeth erect or spreading, to 5 mm long; fruiting pedicels to 3 cm long; seeds ca. 65 per fruit, yellow, flattened, the testa hardened 2 × 3 mm. Figures 2F, 3, 4.

Dentro de la sección *Simplicipila* esta especie presenta pubescencia áspera, castaño-amarillenta y con los tricomas de base ligeramente expandida, flores solitarias, corolas mayores de 9 mm de longitud; bayas oblongas, cónicas u ovoides, sin células pétreas.

The species has coarse yellowish brown pubescence. Many of the hairs have slightly expanded bases. The mature fruits are conical or ovoid.

Distribution. Venezuela, Colombia, and Peru. Ravine sides and disturbed sites in cloud forests, 800–3300 m elevation. (Map, Fig. 4.) Flowering and fruiting throughout the year.

Representative specimens examined. VENEZUELA. **Distrito Federal:** Alrededor de las Aguaditas, 2 km al norte de la Colonia Tovar, 1970–2000 m, Steyermark & Delascio 123500 (MO, VEN). **Aragua:** Colonia Tovar, Benítez et al. 4236 (MY). **Lara:** Parque Nacional Yacambú, Fernández 3697 (MY). **Mérida:** Monte Zerpa, 1970–2050 m, Benítez & Otero 4609 (MY). **Miranda:** Silla de Caracas, quebrada Los Palos Grandes, 1700–1800 m, Morillo & Manara 1600 (MY, VEN). **Táchira:** Selva nublada, río Quinimarí, arriba de Las Copas, 2500–2800 m, Steyermark et al. 100742 (MY, VEN). **Trujillo:** Selva nub-

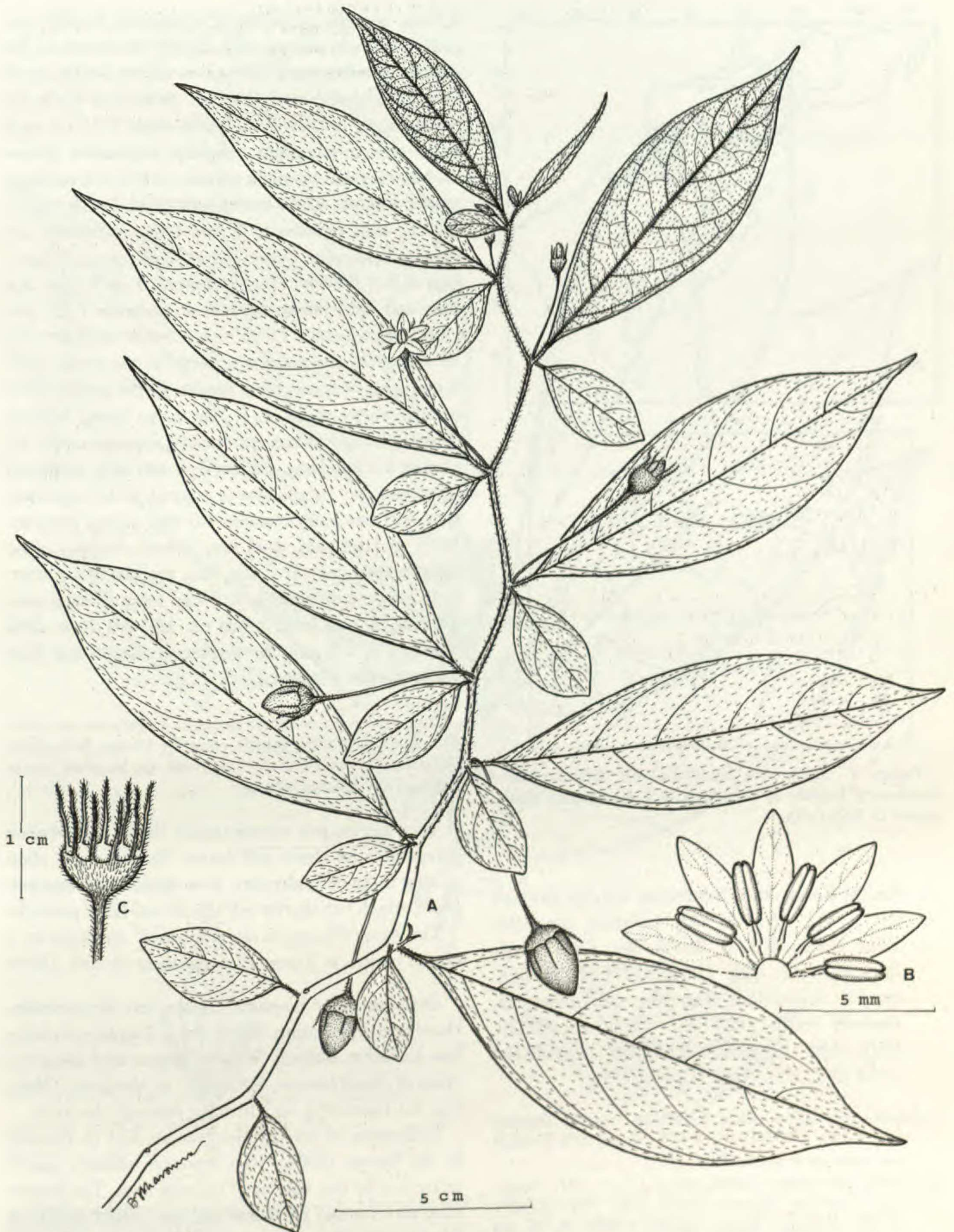


Figure 3. *Lycianthes acutifolia*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Fructing calyx. After Benítez 4236 (MY).

lada virgen de las montañas de Misisí, carretera Trujillo-Boconó, 2200–2400 m, *Steyermark & Manara 125326* (VEN). **Yaracuy:** Sierra de Aroa, 9 km W de San Felipe, 1100–1500 m, *Liesner & González 10038* (VEN). **Zulia:**

Dist. Perijá, on international boundary, headwaters of río Guasare, 2700–3300 m, *Wood & Berry 85* (VEN).

2. *Lycianthes amatitlanensis* (Coulter & J. D.

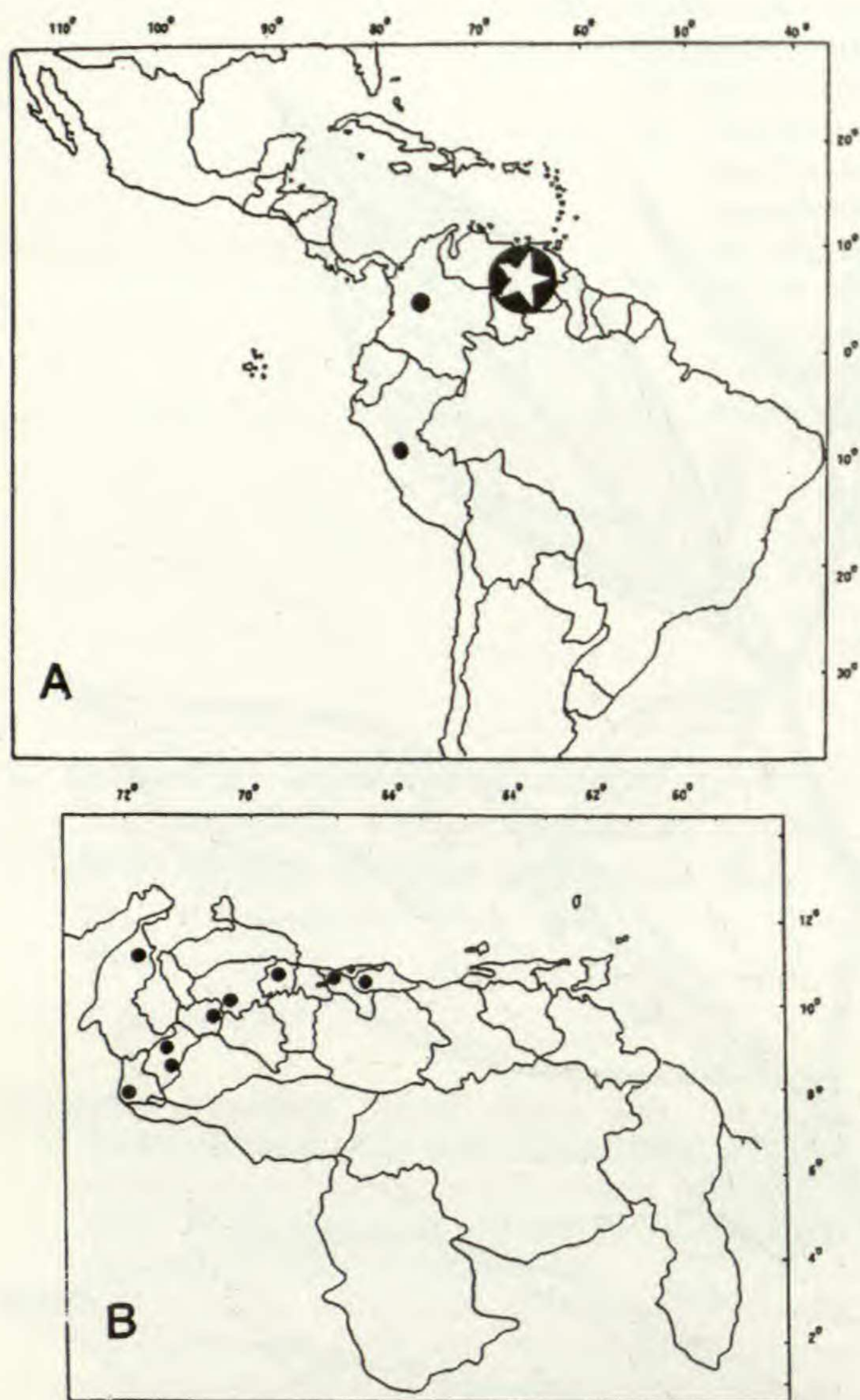


Figure 4. *Lycianthes acutifolia*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Smith) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 441. 1919 [1920]. *Solanum amatitlanense* Coult. & J. D. Smith, Bot. Gaz. (Crawfordsville) 37: 420. 1904. SYNTYPES: Guatemala. Amatitlán, Barranca de Eminencia, *Donnell Smith 1457* (F, = F photo 49339, GH); Alta Verapaz: Cubilquitz, *Tuerckheim 7753* (NY, US), *8488* (C, NY, US).

Lycianthes ulei Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 437. 1919 [1920]. TYPE: Brazil. *Ule 9764* (B not seen, = F photo 2592, NY).

Lycianthes ulei subsp. *dolichodonta* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 438. 1919 [1920]. TYPE: Ecuador. Balao, *Eggers 14409* (A, M not seen, US).

Lycianthes ulei var. *strigulosa* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 438. 1919 [1920]. TYPE: Ecuador. S. Miguel, *Sodirol 114/46* (B not seen).

Subshrub 1–2 m long, erect or arching and wand-like; stems terete, puberulent; pubescence of coarse, simple, erect, or ascending hairs, often suffused with purple. **Leaves** unequal-geminate, ovate, 14–23 × 4–

8.5 cm, apically cuspidate or acuminate, basally narrowed, strongly oblique and slightly decurrent on the petiole, membranous, dark green above, bright green beneath, glabrate on both sides, pubescent along the nerves, more densely so beneath, veins 7–10 on each side, arcuate-ascending, slightly impressed above, slightly elevated beneath; petioles to 0.8–1.5 cm long, mostly strigose; minor leaves subrotund, 1–1.5 × 0.5–0.7 cm with petioles to 5 mm long, sometimes caducous before the major leaves. **Inflorescences** fascicles of 2–5 flowers. **Flowers** diurnal, 1 or 2 open at a time and held below the leaves; pedicels 7–12 mm long, strigose; calyx 1.5–2 × 3–3.5 mm, strigose, with 10 subapical unequal linear teeth in one series, 2.5–3 mm long, strigose, often hidden in the pubescence; corolla white, rotate, 6–9 mm long, lobed halfway down, sparingly pubescent outside; stamens equal, filaments 1.5 mm long, anthers 3–4 mm long, narrowed apically; ovary subglobose or conical, 1–1.5 mm long, style 5–6 mm long, exerted 1.5 mm, stigma capitate. **Berry** globose, red, 6–8 mm across, lacking stone cells; fruiting calyx 6–7 mm long, applied to the berry, teeth erect or spreading, to 5 mm long; fruiting pedicel 13–15 mm long; seeds ca. 100 per fruit, dark brown, 1 × 1.5 mm, the thickened margin less than 0.5 mm wide. Figures 2J, 5.

Especie con pubescencia estrigosa y densa en sus tallos y hojas, los pedicelos florales entre 7 y 12 mm de longitud y los dientes del cáliz de 2.5–3 mm de longitud, bayas globosas sin células pétreas.

This species has conspicuously dense and strigose pubescence on stems and leaves. Its stems are often arching in forest understory. It is similar to *L. inaequilatera*, which has shorter calyx teeth and floral pedicels.

The name "*Solanum amatitlanense*" appeared as a nomen nudem in Enum. Pl. Guatemala (4: 110. 1895).

Distribution. Venezuela, Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Bolivia. Wooded slopes and along ravines of cloud forests, 500–1200 m elevation. (Map, Fig. 6.) Flowering and fruiting through the year.

Pollination of this species was studied in Panama by de Nevers (1986), who reported vibratile pollen extraction by two species of halictid bees. The flowers have no odor and no nectar and are visited mainly in the morning when they are illuminated by sunlight.

Representative specimens examined. VENEZUELA. **Sucre:** Camino a Mundo Nuevo-Manacal, 18–20 km NW of Irapa, 500–700 m, *Morillo 2519* (VEN); Peninsula de Paria, *Knapp & Mallet 6766* (BH, MY), *Steyermark & Liesner 120772* (MO, NY, VEN), *Steyermark & Rabe 96125* (P, VEN), *Steyermark et al. 121528* (VEN), *121593* (VEN). **Yaracuy:** Sierra de Aroa, río Carabobo, 800–1200 m, *Liesner & González 9773* (VEN).

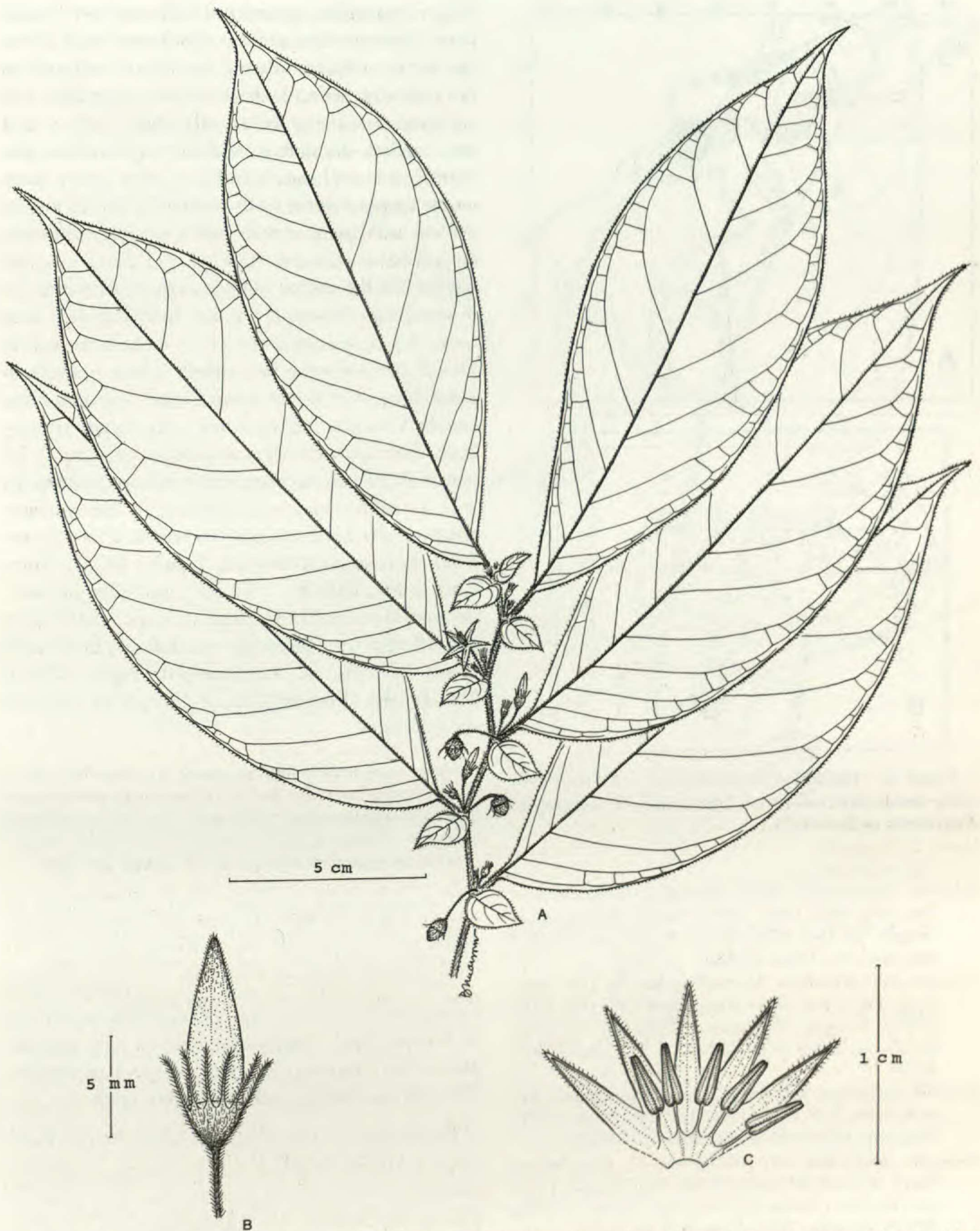


Figure 5. *Lycianthes amatitlanensis*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower. After Steyermark 121528 (VEN).

3. *Lycianthes asarifolia* (Kunth & Bouché) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 423. 1919 [1920]. *Solanum asarifolium* Kunth & Bouché, Index Sem. Hort. Berol. p. 10. 1845. *Solanum violifolium* var. *asarifolium* (Kunth & Bouché) Hassl., Repert. Spec. Nov.

Regni Veg. 15: 221. 1918. TYPE: cultivated in Berlin from seed from Caracas (holotype, B destroyed, = F photo 2562).

Solanum violaeifolium var. *majus* Dunal, in DC., Prodr. 13(1): 164. 1852. TYPE: Bolivia. Santa Cruz, *d'Orbigny* 619 not seen.

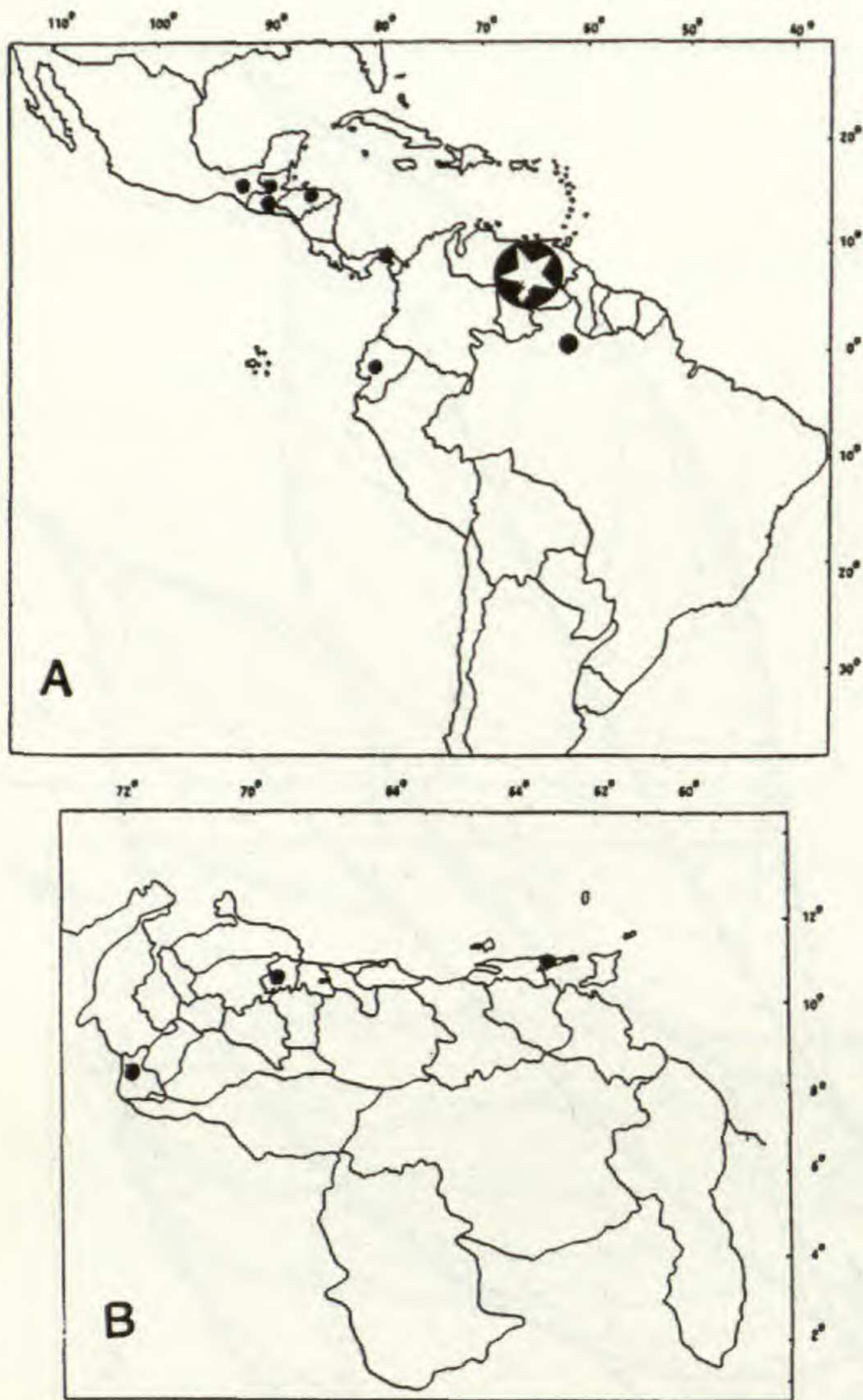


Figure 6. *Lycianthes amatitlanensis*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Solanum chodatianum Huber, Bol. Mus. Paraense Hist. Nat. 4(4): 602. 1906. TYPE: Brazil. Villa de Contamana, 15 Dec. 1898, Huber 1336 (holotype, MG not seen, = F photo 45292).

Solanum violaefolium fo. *lilaciniflora* Hassl., Trab. Mus. Farm. Fac. Cienc. Med. Buenos Aires 21: 106. 1909. TYPE: Paraguay. Pilcomayo, Rojas 605 not seen. [Synonymy taken from Barboza & Hunziker (1992: 31).]

Solanum violifolium var. *majus* fo. *chacoense* Hassl., Repert. Spec. Nov. Regni Veg. 15: 220. 1918. TYPE: Paraguay. Lower Pilcomayo, Rojas 275 (MO).

Solanum violifolium var. *asarifolium* fo. *decadontum* Hassl., Repert. Spec. Nov. Regni Veg. 15: 221. 1918. SYNTYPES: Paraguay. Pilcomayo River, Morong 920 (G not seen, MO); Rojas 605 not seen.

Creeping herb, stems slender, sparingly pubescent, rooting at the nodes, stoloniferous; pubescence of weak, collapsing, mostly erect, simple hairs. Leaves solitary, ovate, 3–10 × 4–10(–15) cm, apically rounded or obtuse, basally deeply cordate, dark green and sometimes shiny above, matte and lighter beneath, membranous, glabrous, veins 3–4 on each side, strongly ascending, sparingly branched; petioles with purplish tones, 3–14 cm

long, canaliculate, sometimes with scattered simple hairs. Inflorescences solitary, the flowers held above the leaves. Flowers diurnal, inodorous, reflexed on the pedicels; pedicels often white or purplish, 4–9 cm long, 0.5–1 mm thick; calyx pale, 3–5 × 3–4 mm, angled, the margin undulate-denticulate, glabrate inside and out, sometimes with sparse hairs on the costas, lateral teeth absent but the 10 nerves evident on drying; corolla white or pale-yellowish, outspread or reflexed, 0.6–1.1 × 1.2–2.2 cm, the margin almost entire; stamens equal, filaments 1–3 mm long, glabrous, anthers held together in a cone, 2.5–3 mm long, the pores extending slightly toward the sides of the anther; ovary conical or subglobose, 1.5–2 mm across, style 5–6 mm long, exerted 1 mm, stigma hardly expanded, subglobose. Berry orange-red, compressed-globose, 8–25 mm × 0.7–2 cm, lacking stone cells; fruiting calyx 5–9 × 11–17 mm, not splitting at the sinuses; seeds ca. 70 per fruit, grayish brown, 2 × 2.5 mm long, the margin thickened. Figures 2E, 7; Saunders, Refug. Bot. 4, t. 255. 1871, as *Solanum asarifolium*; Martius, Fl. Brazil 10, t. 4, 12. 1846 (calyx and stamens), as *Solanum asarifolium*; Benítez de Rojas, 1974: fig. 12; Steyermark & Huber, 1978, t. 288; Huber, 1906: 603, fig. 7 (flower), as *Solanum chodatianum*.

Única especie de hábito prostrado y estolonífero de todas las conicidas de *Lycianthes* en Venezuela, presenta sus hojas conspicuamente cordiformes, las flores solitarias colgantes sobre pedúnculos erectos y los cálices edentados, bayas comprimido-globosas sin células pétreas.

Common names and uses. “Ajicillo,” “Barba de Tigre,” “Childa,” “Huevo de Sapo,” “Nicua.” Fruits are eaten out of hand and also made into jams.

This is the only species with a prostrate habit among Venezuelan species of *Lycianthes*, presenting its conspicuously cordiform leaves on erect petioles and solitary flowers deflected on erect peduncles. The calyces usually lack noticeable teeth.

Distribution. Venezuela, Bolivia, Peru, Paraguay, southern Brazil, and northeastern Argentina. Deciduous and semi-deciduous woods near moist places, 50–1000 m. Also a component of adventive and weedy vegetation in croplands. (Map, Fig. 8.) Flowering and fruiting throughout the year.

This species is similar to *Lycianthes repens* (Spreng.) Bitter of southeastern Brazil, which is said to differ (Bitter, 1920: 426) in having smaller leaves, shorter stalks, and distinctive hairs. We have seen only two collections that were cited by Bitter under this name. One of these, *Dusén 11315* (F, MO) from Paraná, Ponta Grossa, has two unequal but well-developed leaves at each node. The

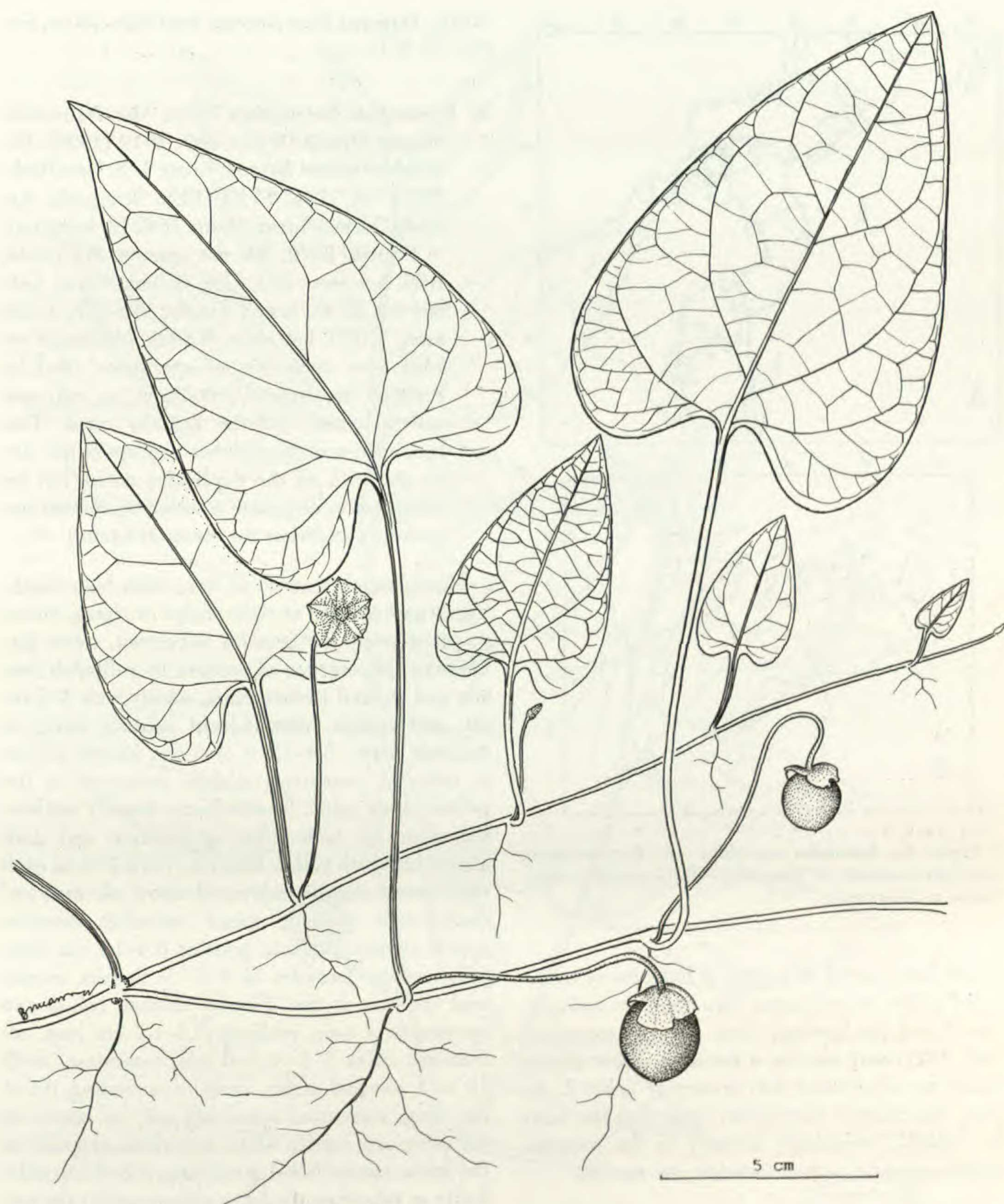


Figure 7. *Lycianthes asarifolia*. Flowering and fruiting stems. After Licata et al. 32 (MY).

other specimen, Pohl 5407 (F), without locality, has solitary major leaves and sessile minor leaves like many plants from elsewhere. The Dusén specimen is the only one we have seen with well-developed, long-petiolate minor leaves. The original description of the basionym, *Boldoa repens* Spreng. (Syst. Veg. 1: 179. 1825) and Bitter's description also note unequally paired leaves. While the Dusén collection does have small leaves and peduncles, except

for the well-developed minor leaves it seems to be conspecific with plants we have identified as *L. asarifolia*. If *L. asarifolia* and *L. repens* are actually the same, then *L. repens* is the prior and correct name. We continue use of *L. asarifolia* for this species, a name that has been used in many publications, rather than substituting the unfamiliar and uncertainly equivalent name *L. repens*. Bitter cited a specimen, "Otto ex hb. Kurt Sprengel," which

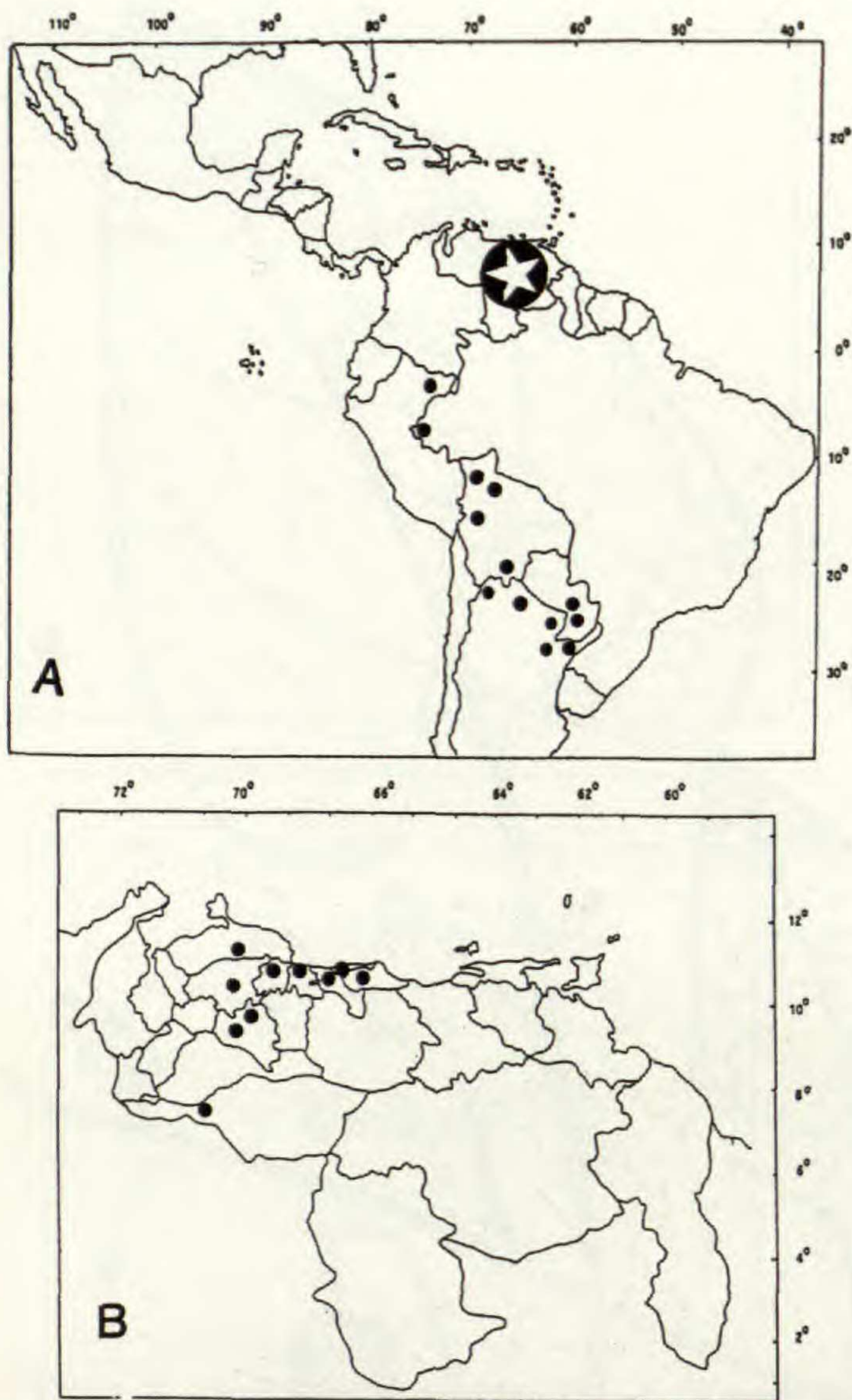


Figure 8. *Lycianthes asarifolia*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

would have served as a type. If *L. repens* is recognized as the correct name, then *Solanum violaefolium* Schott (in Sprengel, Syst. Veg. 4 (appendix): 403. 1827) may also be a synonym. Bitter placed *Solanum violaefolium* into synonymy under *L. repens*, but Schott's description notes that the calyx is "10fidis," seemingly contrary to the truncate, nearly edentate calyces found in our species.

Representative specimens examined. VENEZUELA. **Distrito Federal:** S Naiguatá, vertiente N de la Cordillera de la Costa, 600–800 m, *Morillo & Manara 2022* (VEN). **Apure:** Boca del Uribante, *Trujillo & Fernández 10597* (MY). **Aragua:** Río Hondo, km 32 carretera hacia Choroni, 800 m, *Benítez & Rojas 3993* (MY). **Carabobo:** La Toma de Valle Seco, Dist. Puerto Cabello, 100–200 m, *Benítez & Pons 4651* (MY). **Cojedes:** Las Tucuraguas, Mpio. Angel Bravo, 700 m, *Delascio & López 12838* (VEN). **Falcón:** Parque Nacional Quebrada de la Cueva El Toro, 600–900 m, *Liesner et al. 7803* (MY, VEN). **Lara:** Barquisimeto, *Saer 263* (VEN). **Miranda:** near río Guaire between Los Palos Grandes and Dos Caminos, 940 m, *Steyermark 60971* (MY, VEN). **Portuguesa:** Carretera Mesa Cavacas-Biscucuy, *Stergios & Aymard 4451* (MY,

PORT). **Yaracuy:** Finca Antonia, San Felipe, 250 m, *Ferrari 790* (MY).

4. *Lycianthes ferruginea* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 339. 1919 [1920]. *Solanum ornatum* Morton, Contr. U.S. Nat. Herb. 29(1): 59. 1944. SYNTYPES: Venezuela. Aragua: Colonia Tovar, *Moritz 1642* (B destroyed, = F photo 2572, BM not seen, = MY photo; HBG not seen, MO, US); Colonia Tovar, *Golmer s.n.* (B not seen); *Fendler 991* (BR, G not seen, GOET not seen, NY-2). [Although we have seen duplicates of specimens cited by Bitter in the original protologue, we only saw one specimen that he actually cited. This specimen accords with our concept of the taxon and with all the duplicates noted, but we chose not to designate a lectotype without opportunity to review the material again.]

Much-branched *shrub* or *vine*, often high-climbing, branches often at right angles or zigzag, young growth densely ferruginous pubescent, stems glabrescent; pubescence of reddish or yellowish sessile and stalked stellate hairs, mostly with 3–5 radii, and simple hairs. *Leaves* solitary, ovate or narrowly ovate, 3.4–12 × 2–6 cm, basally obtuse or rounded, sometimes slightly decurrent on the petiole, apex acute, membranous, densely stellate-pubescent on both sides, glabrescent and dark above, brownish yellow beneath, veins 3–4 on each side, mostly slightly impressed above, elevated and conspicuous beneath, minor reticulate venation mostly evident beneath; petioles 0.4–1.7 cm long. *Inflorescences* fascicles of 2–4(–5) flowers, mostly near the branch tips. *Flowers* diurnal, one or two opening at a time; pedicels 0.8–1.7 cm long, tomentose; calyx 3–7 × 3–8 mm, tomentose, teeth 10 in 2 unequal series, erect or spreading, 0.5–4 mm long, sometimes appearing only as costas on the calyx cup; corolla white, sometimes greenish on the lobes, rotate, 0.9–1.5 cm long, 1.8–3 cm wide, entire or subentire, the lobes conspicuously thicker, glabrous outside overall, the lobes sometimes minutely ciliolate with reduced curved hairs, sometimes with small tufts of stellate hairs on the lobe tips, glabrous within; stamens unequal, 4 filaments 1–2 mm long, the fifth 2–4.5 mm long, anthers 2.5–3 mm long; ovary ovoid, 2–4 × 1–3 mm, glabrous, style 6–7 mm long, glabrous, exerted 1 mm, stigma subclavate. *Berry* orange-red, subglobose, 10–20 mm across, with 2–4 stone cells; fruiting calyx slightly accrescent, the cup 4–6 mm long, applied to the berry, sometimes splitting irregularly, the teeth slightly reflexed, not accrescent; seeds ca. 36

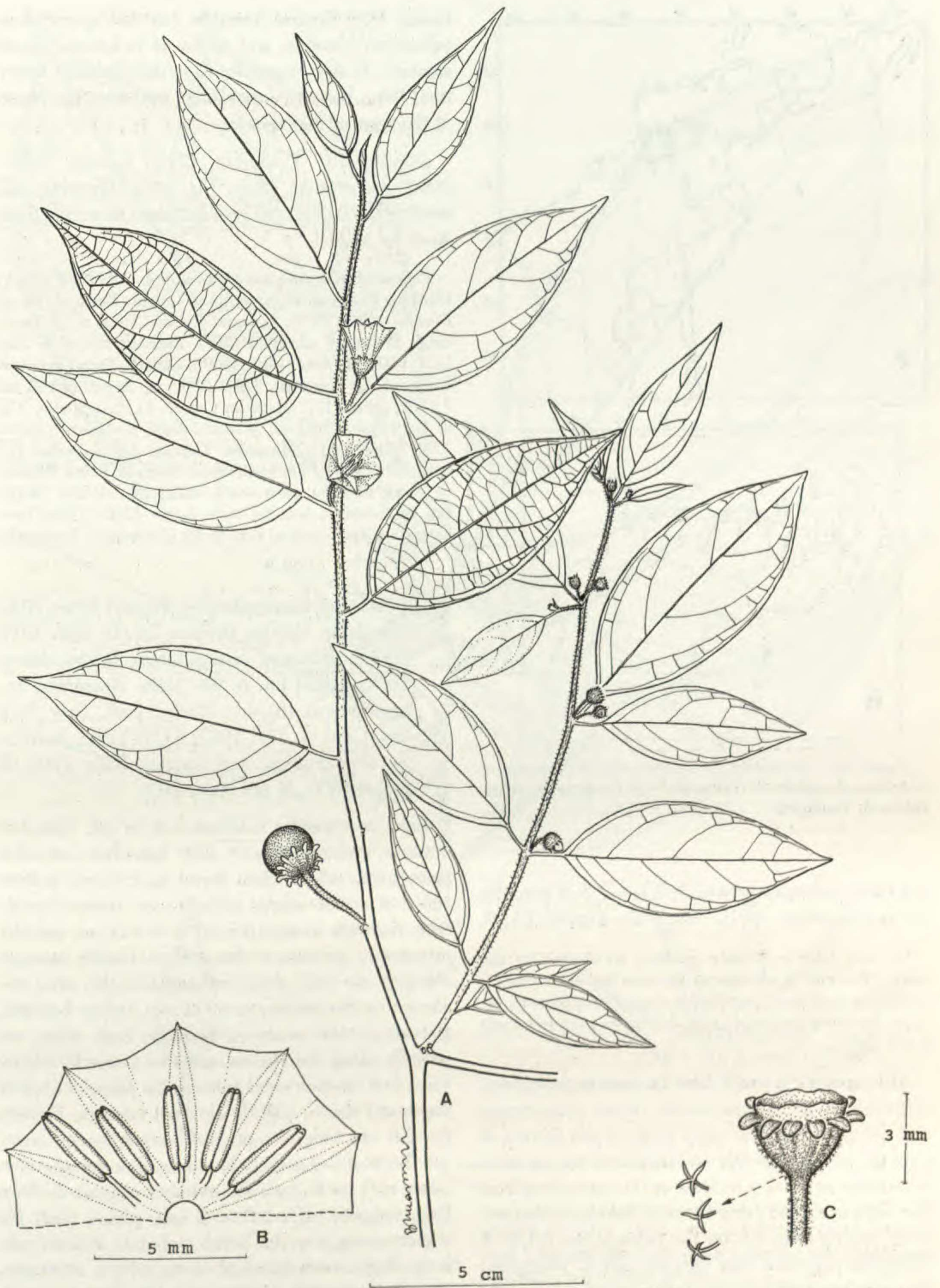


Figure 9. *Lycianthes ferruginea*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Fruiting calyx. After Benítez 5148 (MY).

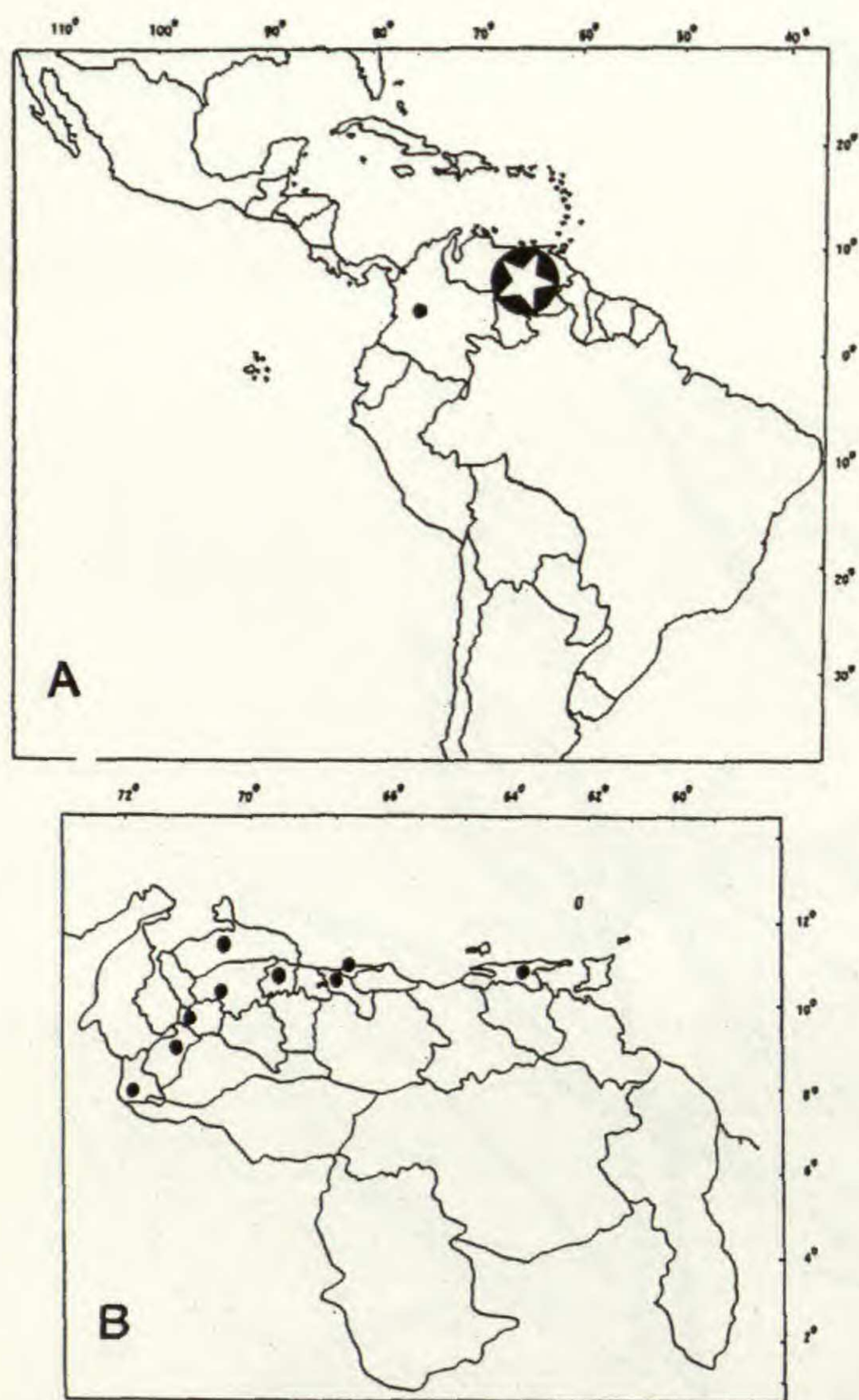


Figure 10. *Lycianthes ferruginea*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

per fruit, yellowish brown, $3-3.5 \times 3.5-4$ mm, the thickened margin ca. 0.7 mm wide. Figures 2A, 9.

En esta especie el cáliz presenta 10 dientes en dos series; la corola generalmente muestra los lobos conspicuamente verdosos y engrosados y el pliegue blanco; las bayas son subglobosas, sin células pétreas o desde 1 hasta 4 por fruto.

This species is much like *Lycianthes pauciflora*, differing in its conspicuously dense pubescence and corolla color. The calyx lobes of the flowers of this species vary greatly in length and appearance, sometimes appearing as short points spreading from the calyx apex and other times as slender tomentose teeth arising from low on the sides of the calyx. A difference between this species and *L. pauciflora* that was not noted in the key to species is in the coloration of the corollas when seen from outside; in *L. ferruginea* the lobes are green and the folds white, while in *L. pauciflora*, the entire surface is white.

This species is also similar to *L. armentalis* J. L.

Gentry from Central America, but that species has pubescent corollas, and so far as is known, equal stamens. It also resembles *L. jelskii* (Zahlbr.) Bitter from Peru, but we cannot judge well from the photo of the type of that species.

Distribution. Colombia. Cloud forests, 1200–2900 m elevation. (Map, Fig. 10.) Flowering and fruiting throughout the year but most flowering from April to August.

Representative specimens examined. VENEZUELA. **Distrito Federal:** El Junquito to Colonia Tovar, 1770 m, *Davidse* 4035 (VEN). **Aragua:** Colonia Tovar to El Aguacatal, *Benítez et al.* 4235 (MY). **Falcón:** Sierra de San Luis, 1500 m, *Demey* (MY-86695, CORO). **Lara:** between Cubiro & La Escalera, 1600–2000 m, *Steyermark et al.* 110242 (MY, VEN). **Mérida:** Caserío El Portachuelo, NW of Guaraque, 2000 m, *Marcano-Berti & López-Palacios* 1758 (MER, MY). **Miranda:** Cortada del Guayabo, *Tamayo* 397 (VEN). **Táchira:** above Betania, below Páramo de Tamá, 2530 m, *Steyermark* 57433 (MY, VEN). **Trujillo:** El Paramito, near Escuque, *Lasser* 1203 (VEN). **Yaracuy:** Los Quinquines, road to La Candelaria, *Diederichs* 173 (VEN).

5. *Lycianthes inaequilatera* (Rusby) Bitter, Abh. Naturwiss. Vereine Bremen 24 (1): 439. 1919 [1920]. *Bassovia inaequilatera* Rusby, Mem. Torrey Bot. Club 6: 90. 1896. *Brachistus inaequilaterus* (Rusby) Rusby, Bull. New York Bot. Gard. 4: 470. 1907. SYNTYPES: Bolivia. Between Tipuani and Guanai, *Bang* 1708 (B not seen, G, M not seen, MO).

Erect or wandlike *subshrub* 1–2 m tall, branches flexuous, arching, strigose, adult branches somewhat glabrescent, ridged, often drying dark brown; pubescence of coarse simple hairs. *Leaves* unequal-geminate, narrowly ovate, $16.5-20 \times 4-6.5$ cm, apically acuminate, sometimes abruptly so, basally strongly oblique, one side obtuse or rounded, the other decurrent on the petiole, membranous, lighter beneath, glabrate or with scattered hairs on both sides, especially along the nerves, more so beneath, ciliate, veins 6–8 on each side, major veins plane or slightly impressed above, slightly elevated beneath; petioles 0.5–0.8 cm long, compressed; minor leaves ovate, $2.3-3.6 \times 1.3-1.6$ cm, subsessile. *Inflorescences* fascicles of (1–)4 flowers. *Flowers* with pedicels 2–3 cm long, strigose; calyx 2.5×2 mm, pilose, teeth 10, slightly unequal in one series, subulate, 0.5–0.7 mm long, strigose; corolla white, rotate, $8-9 \times 9-10$ mm, lobed $\frac{1}{2}-\frac{1}{3}$ way down, pilose outside; stamens equal, filaments 3.5 mm long, anthers 2.5–3 mm long; ovary ovoid, $1 \times 0.5-0.6$ mm, style 6.5 mm long, exerted 2 mm, stigma capitate. *Berry* red, subglobose, 5–6 mm across, without stone cells; fruiting calyx accrescent, the cup 3–4.5 mm long, the teeth slightly ac-

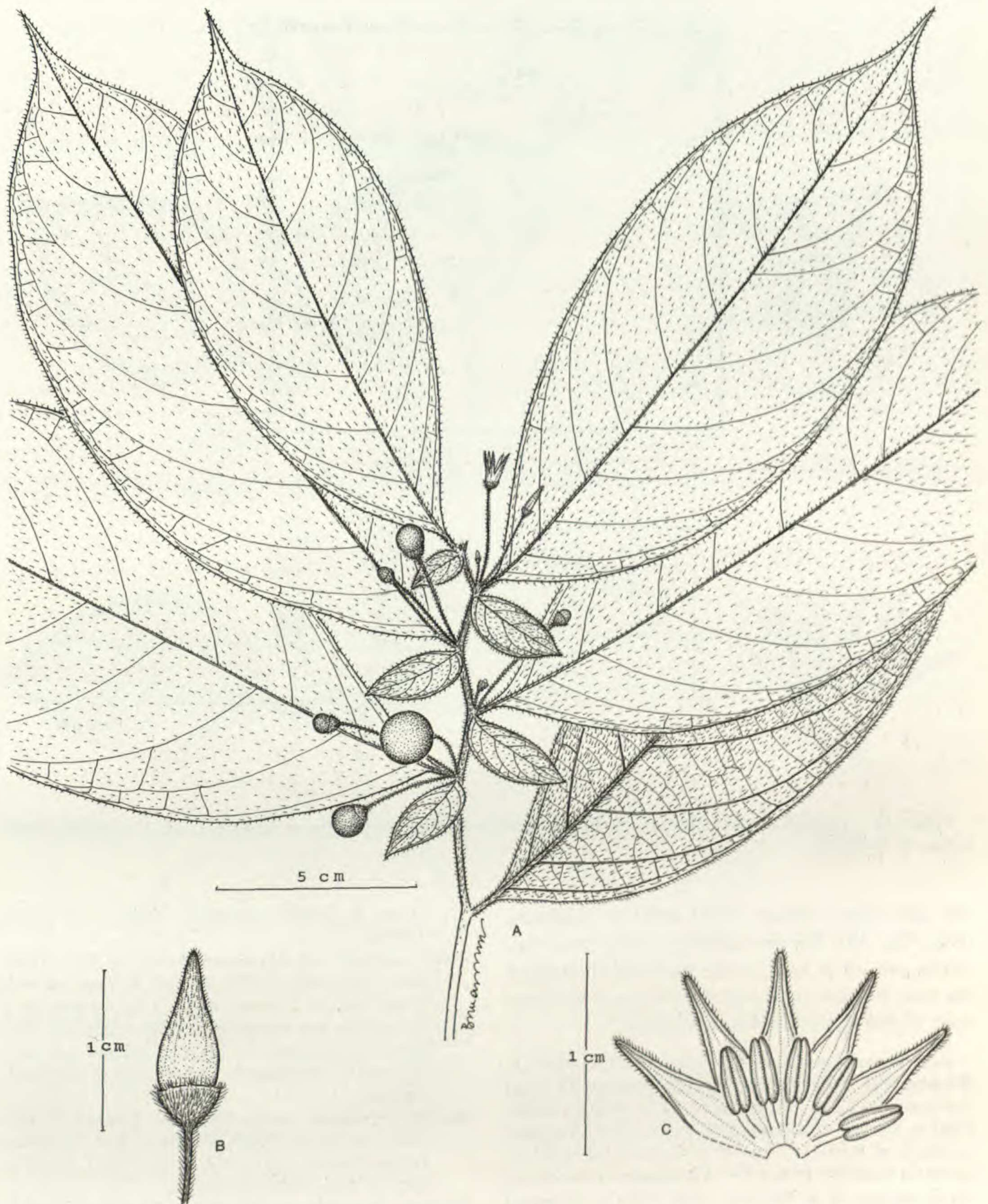


Figure 11. *Lycianthes inaequilatera*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower. A. After Stergios et al. 6360 (MY); B, C. After Davidse 18899 (VEN).

crescent, fruiting pedicels 2 mm long; seeds ca. 70 per fruit, yellowish brown, 1.5–1 mm across, the conspicuously thickened margin 0.5 mm wide. Figures 2I, 11.

Se caracteriza por ser pubescente, con hojas menores conspicuas, los dientes del cáliz en número de 10, ligeramente desiguales, en una serie y subulados, los cuales

son generalmente poco conspicuos en fruto, bayas subglobosas, sin células pétreas.

This species closely resembles *L. amatitlanensis*, from which it differs in its lesser pubescence and shorter calyx teeth, which are usually less conspicuous in fruit, and longer pedicels.

Distribution. Venezuela and Bolivia. Cloud for-

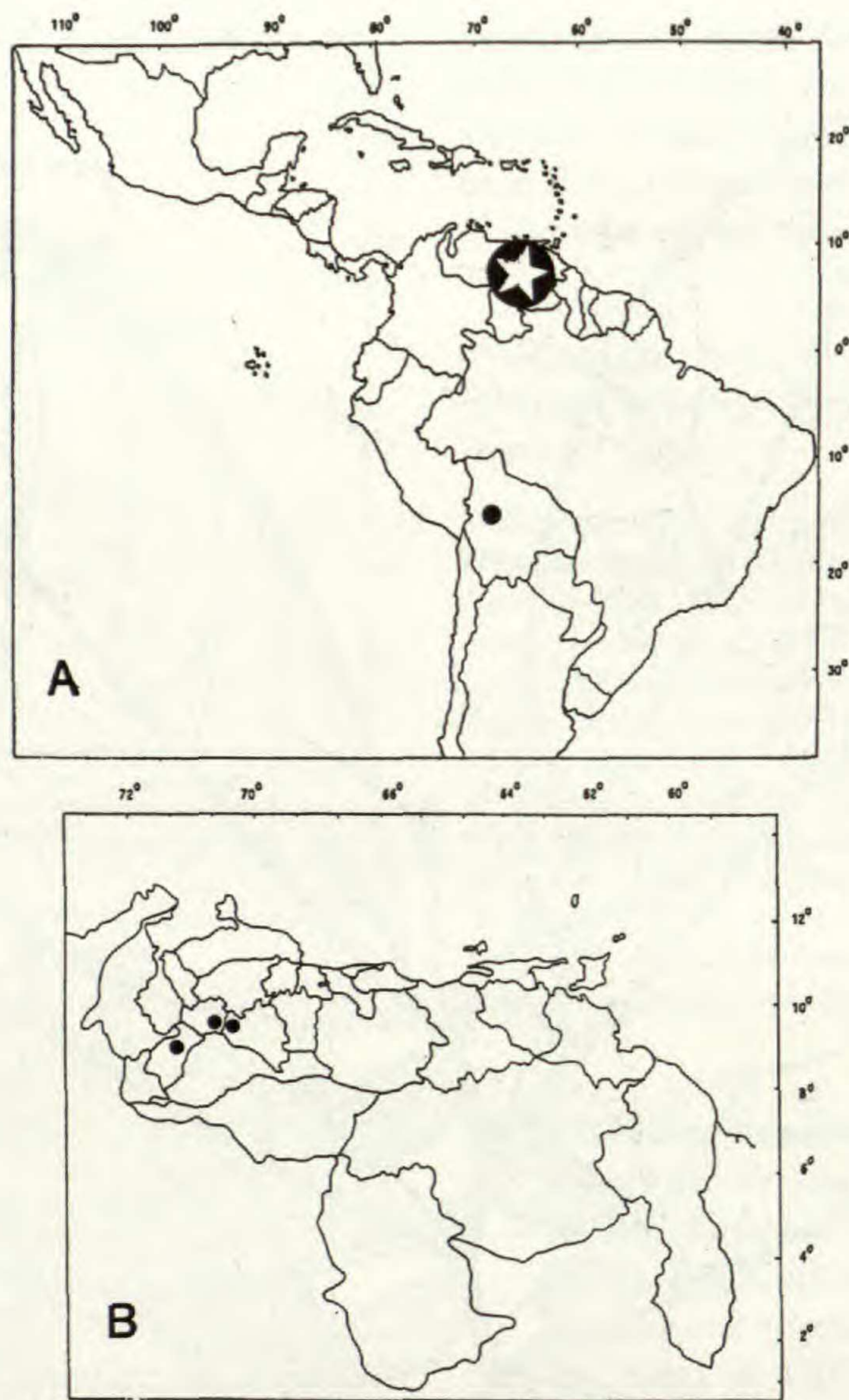


Figure 12. *Lycianthes inaequilatera*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

ests and along ravines, 1500–1900 m elevation. (Map, Fig. 12.) The six collections seen from Venezuela are all in fruit, made scattered throughout the year. Further collecting should reveal the presence of this species in other countries.

Representative specimens examined. VENEZUELA. **Mérida:** Dist. Andrés Bello, between quebrada El Trigal and quebrada Zerpa, 10–14 km SE of La Azulita, 1600–1900 m, *Davidse & González 18899* (NY, VEN). **Trujillo:** 13 km E of Boconó, 1 km W of Guaramacal, 1600 m, *Liesner et al. 12833* (MY, VEN). **Portuguesa:** Dist. Sucre, Los Paramitos, SE of Biscucuy, 1000–1500 m, *Stergios et al. 6360* (MY, PORT).

6. *Lycianthes lenta* (Cav.) Bitter, *Abh. Naturwiss. Vereine Bremen* 24(1): 364. 1919. *Solanum lentum* Cav., *Icon.* 4: 4, plate 308. 1797. *Solanum virgatum* Lam. var. *lentum* (Cav.) O. E. Schulz, in Urban, *Symb. Antill.* 6: 189. 1909. TYPE: cultivated Madrid, seed from Mexico (holotype, MA).

Solanum cumanense Roem. & Schultes, *Syst. Veg.* 4: 662. 1819. TYPE: Venezuela. Cumaná, *Humboldt* 71 (ho-

lotype, P, = IDC microfiche 4316, = F photo, 002896).

Solanum lentum var. *echinatum* Dunal, in DC., *Prodr.* 13(1): 173. 1852. TYPE: Mexico. Without collector (G not seen, = F photo 34120). [The typification of this species was interpreted by Nee (1986: 97) to be based on specimens of Sesse & Mocino now at F, MA, and G, including the one of which we have seen a photo.]

Solanum sylvaticum sensu Schlecht., *Linnaea* 5: 112. 1830, non Dunal (1852), fide Bitter, *Abh. Naturwiss. Vereine Bremen* 24(1): 364. 1919 [1920]. Based on material from Veracruz, Mexico.

?*Solanum quadriflorum* M. Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* 12(1): 139. 1845. TYPE: Mexico. *Galeotti 1231* (holotype, BR not seen; isotype, P not seen, = F photo 39198).

Solanum declinatum Sessé & Moç., *Fl. Mex.* ed 2: 54. 1893 [1894]. SYNTYPES: Mexico. Teuzitlan specimen not indicated. [Nee (1986: 97) cited as authentic material: *Sessé & Mociño 1525* (F, MA not seen, = F photo 48223) and *Sessé & Mociño 5366* (F, MA not seen, = photo 48235).]

Solanum lambii Fernald, *Bot. Gaz. (Crawfordsville)* 20: 536. 1895. TYPE: Mexico. Sinaloa: Villa Union, *Lamb 446* (holotype, GH not seen; isotype, MO).

Solanum nocturnum Fernald, *Proc. Amer. Acad. Arts* 35:

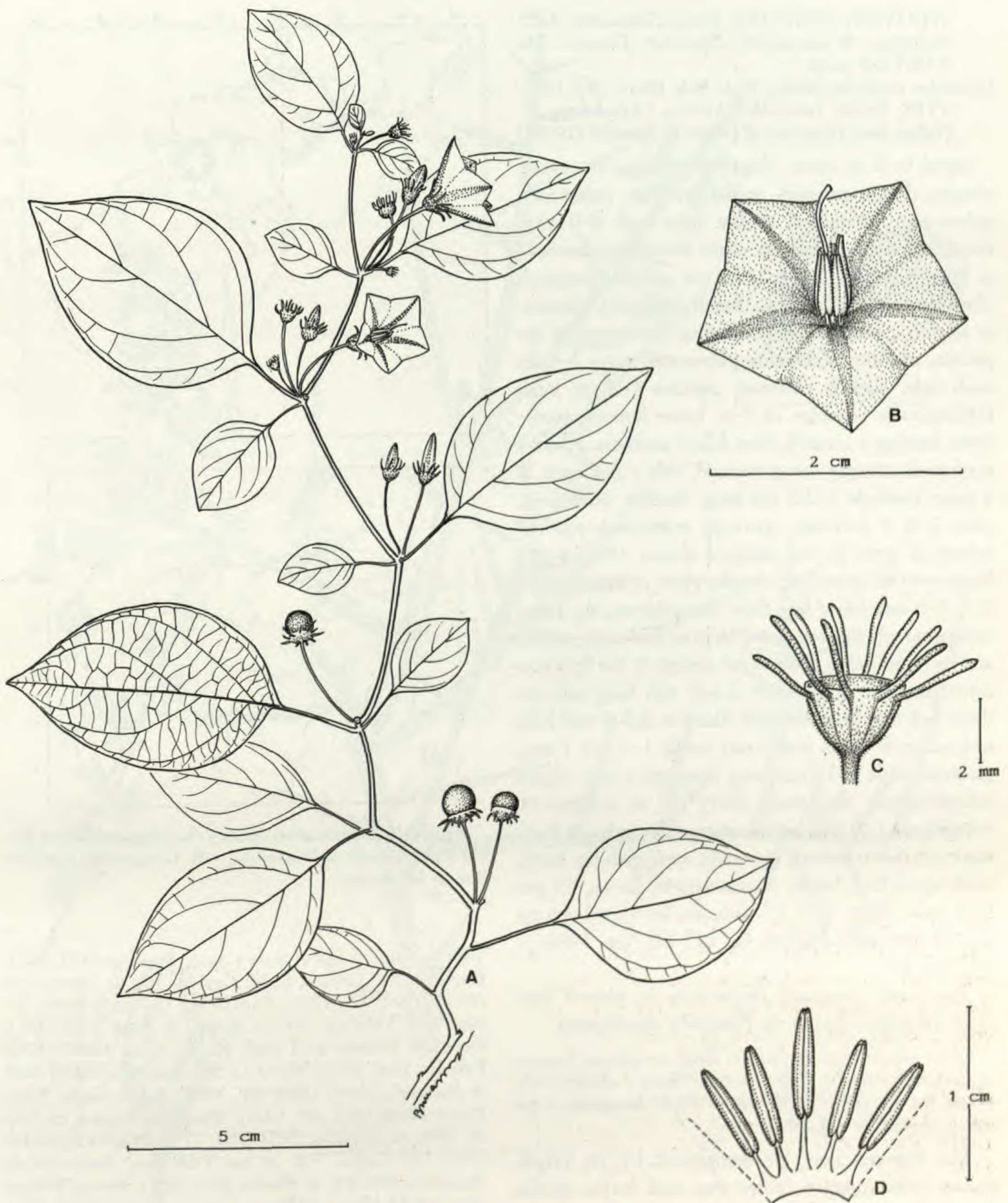


Figure 13. *Lycianthes lenta*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Flower bud.—D. Stamens inserted on corolla. After Bunting 4433 (MY).

570: 1900. SYNTYPES: Mexico. Oaxaca: Palmer 533 (GH not seen); Tehuantepec, Seler 1625 (GH not seen).

Lycianthes lenta var. *endopsila* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 367. 1919 [1920]. SYNTYPES: Venezuela. Caracas, Humboldt 748 (B not seen); Vargas s.n. (lectotype, designated here, US-601441).
Solanum virgatum Lam. var. *caracasenum* O. E. Schulz,

in Urban, Symb. Antill. 6: 190. 1909. TYPE: Venezuela. Near Cura, Humboldt 748 (holotype, P).

Lycianthes lenta var. *scotinophila* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 367. 1919 [1920]. TYPE: Venezuela. Valle del Aragua bei San Mateo, Otto 788 (holotype, B destroyed).

Lycianthes pauciflora (Vahl) Bitter subsp. *tobagoensis* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 343.

1919 [1920]. SYNTYPES: Tobago. *Broadway* 4523 (holotype, B destroyed); Trinidad, *Crueger* 148 (GOET not seen).

Lycianthes variifolia Standl., Field Mus. Bot. 4: 259. 1929.
TYPE: Belize. Tower Hill, *Karling* 13 (holotype, F).
[Taken from synonymy of Gentry & Standley (1974).]

Shrub to 3 m, erect, climbing or sprawling, stems slender, drying greenish, young branches pubescent; pubescence of stalked, stellate hairs with 4–6 rays. *Leaves* solitary or geminate, ovate, sometimes narrowly or broadly so, 4.4–10 × 2.6–5 cm, apically rounded, obtuse, or short-acuminate, basally rounded, truncate or slightly cordate, sometimes short-decurrent on the petiole, membranous, softly pubescent, veins 3–4 on each side, slightly elevated; petioles 1–2 cm long. *Inflorescences* fascicles of 5 or fewer flowers, sometimes leaving a cicatrix from fallen pedicels. *Flowers* nocturnal, strongly sweet-scented, only a few open at a time; pedicels 1–2.5 cm long, slender, pubescent; calyx 3–4 × 3–5 mm, sparingly pubescent, with 10 subapical teeth in two unequal series, 1–2(–3) mm long, erect or spreading; corolla white or bluish, 1.5–3 × 3–5 cm, lobed less than 1/3 way down, the lobes conspicuously thicker, puberulent in bud with stellate and reduced hairs, glabrescent except at the tips; stamens unequal, 4 filaments 1.5–2 mm long and anthers 3–4 mm long, the fifth filament 3.5–8 mm long and anther 5–6 mm long; ovary ovoid, 1–1.5 × 1 mm, glabrous, style 8–12 mm long, exerted 2 mm, stigma subemarginate or clavate. *Berry* red or orange-red, subglobose, 6–9 mm across, stone cells lacking; fruiting calyx 6–8 mm long, generally applied to the berry, teeth spreading, hardly accrescent; seeds ca. 35 per fruit, pale yellow, 2 × 2.5 mm, the thickened margin ca. 0.5 mm wide. Figures 1C, 2C, 13; Nee, 1986: p. 101. fig. 10.

The name *Solanum nocturnum* is placed into synonymy here based on Fernald's description.

Es de amplia distribución en áreas de alturas bajas y se caracteriza por sus tallos castaño-claros y ramificación densa, los dientes del cáliz en dos series desiguales y los frutos carecen de células pétreas.

The species may be recognized by its bright brown stems, dense branching, and large corolla diameters.

Distribution. Mainly Caribbean in distribution: Mexico, Belize, Guatemala, El Salvador, Nicaragua, Trinidad and Tobago, Cuba; Venezuela. Deciduous woods and thickets, sea level to 500 m. Often near the sea, but actually of wide distribution in medium and low elevations. (Map, Fig. 14.) The species flowers and fruits throughout the year.

Representative specimens examined. VENEZUELA. **Apure:** Parque Nacional Santos Luzardo, isla El Vapor, 40 m, *Duno et al.* 184 (MY). **Aragua:** Ocumare de La Costa, 0–400 m, *Badillo* 1816 (MY); Carretera Cagua–La

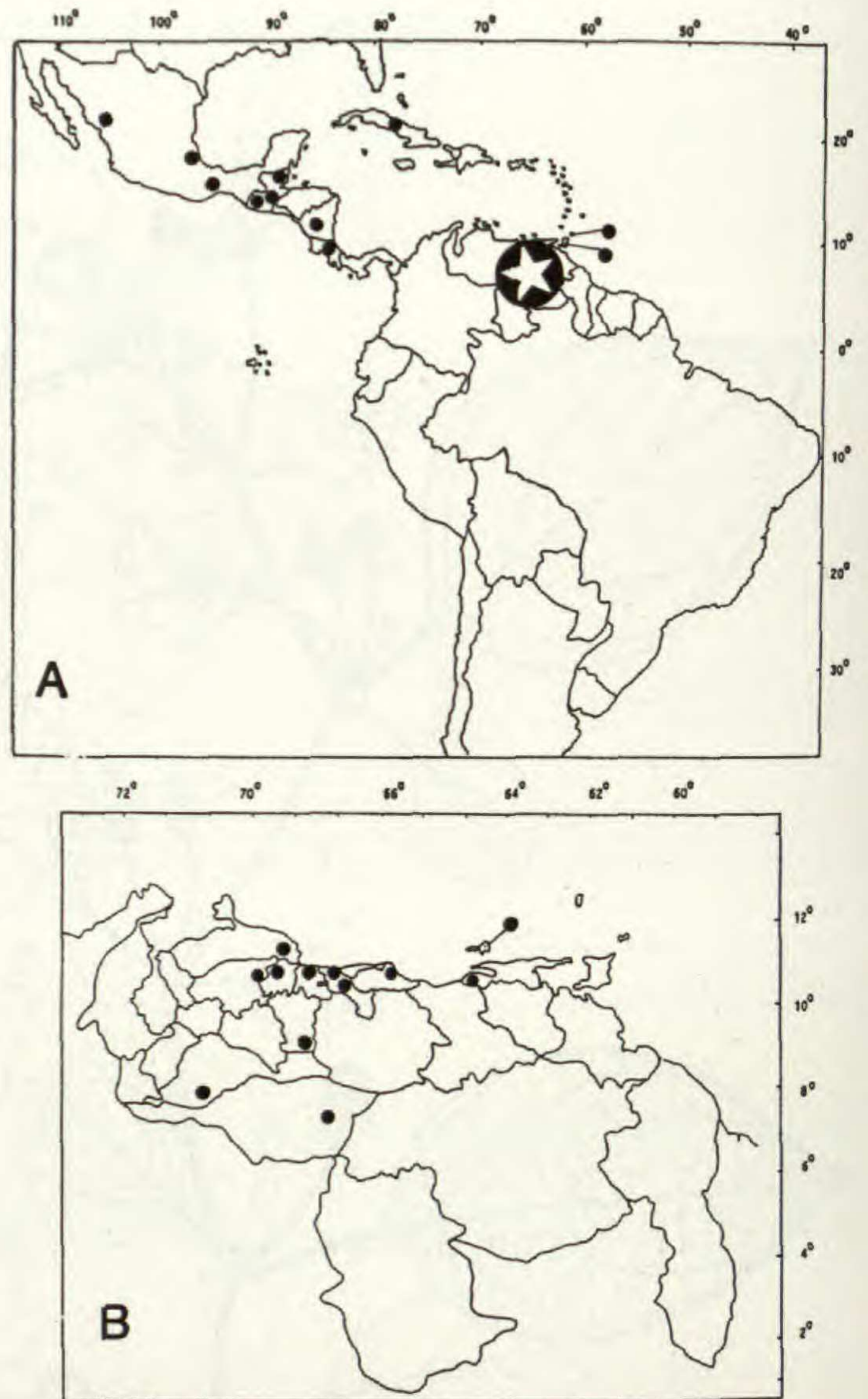


Figure 14. *Lycianthes lenta*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Villa de Cura, 4 km al S de Cagua, *Bunting* 4433 (MY). **Barinas:** Río Caparo, E del Cantón, 100 m, *Steyermark* 102180 (MO, NY, VEN). **Carabobo:** Quebrada María Teresa, Dist. Valencia, 500 m, *Benítez & Rojas* 3214 (MY). **Cojedes:** Entrada a El Baúl, *Trujillo et al.* 16662 (MY). **Falcón:** Dist. Silva, NE of La Soledad, 5 m, *Steyermark & Manara* 110995 (MO, NY, VEN). **Lara:** Santa Rosa, *Pittier* 13088 (MO, NY, VEN). **Miranda:** Paparo, río Chico, 10 m, *Aristeguieta* 3994 (MO, VEN). **Nueva Esparta:** Cerro Los Cedros, SW of San Francisco, Península de Macanao, 100–300 m, *Benítez* 2614 (MY). **Sucre:** Parque Nacional Mochima, El Tacal, *Cumana* 1850 (IRBR, MY). **Yaracuy:** Finca Los Apamates, La Llanada, between Urama & San Felipe, *Romero* 486 (MY). **Zulia:** Carretera Caja Seca–Bobures, *Bunting* 5808 (MO, VEN, VZU).

7. *Lycianthes lycioides* (L.) Hassl., *Annuaire Conserv. Jard. Bot. Genève* 20: 181. 1917. *Solanum lycioides* L., *Syst. Nat.* ed. 12, 2: 174. 1767; *Mantissa Pl.* 1: 46. 1767. TYPE: Peru. LINN 248.48 (lectotype, designated by Knapp & Jarvis (1990)).

Solanum lycioides var. *tomentosa* Dunal, *Hist. Nat. Solanum* 174. 1813. *Solanum candicans* Dunal, *Sol. Syn.*

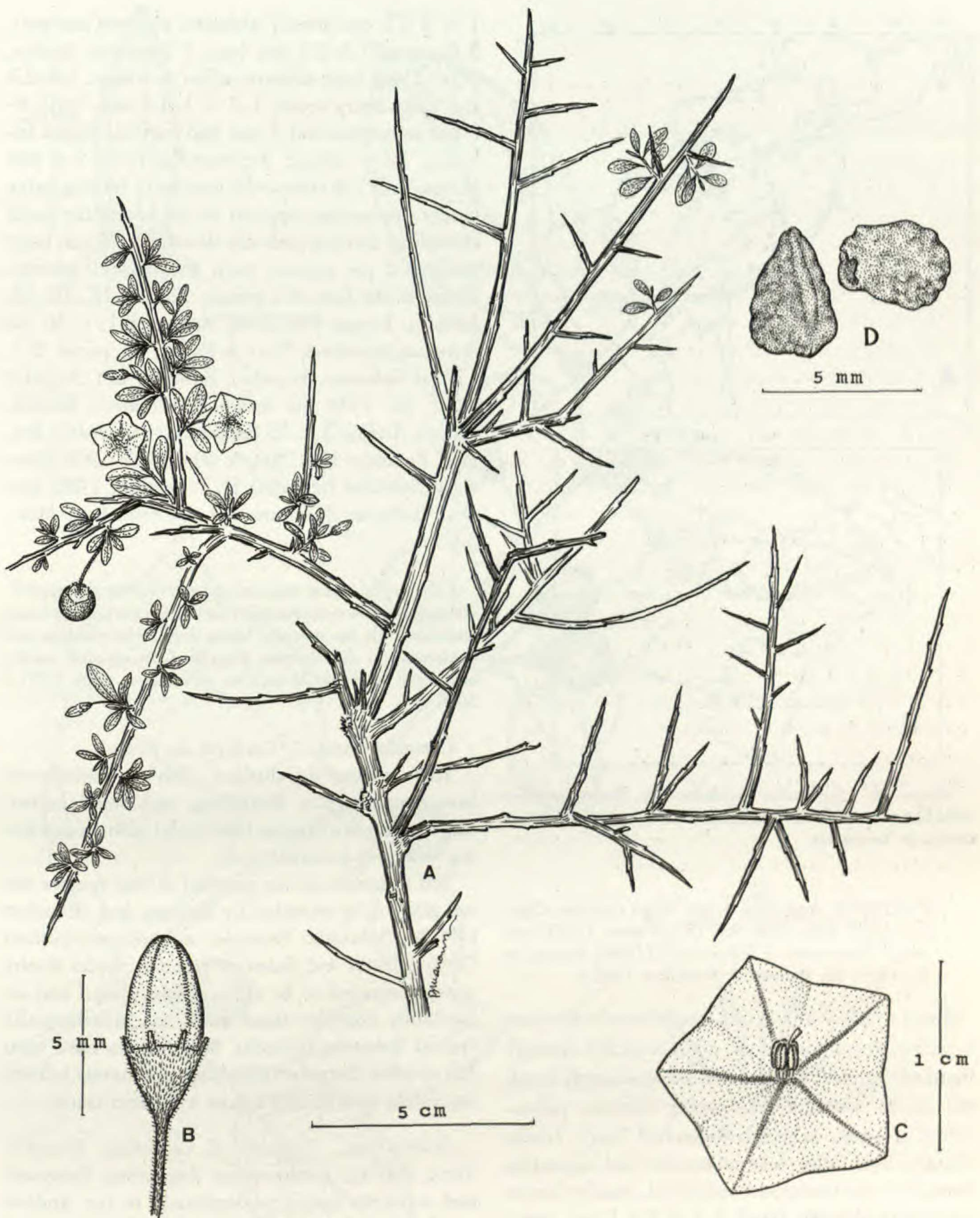


Figure 15. *Lycianthes lycioides*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower.—D. Pyrenes (seeds enclosed in sclerenchyma). After Benítez 5373 (MY).

23. 1816. *Lycianthes candicans* (Dunal) Hassl., *Annuaire Conserv. Jard. Bot. Genève* 20: 181. 1917. *Lycianthes lycioides* subsp. *tomentosa* (Dunal) Bitter, *Abh. Naturwiss. Vereine Bremen* 24(1): 327. 1919 [1920]. Based on *Solanum lycioides* Ruiz & Pav., *Fl. peruv.* 2: 41, 5. 177b, non L. TYPE: Peru. Huanuci & Tarmae (G not seen, = F photo 34114, MPU not seen).

Solanum phillyreoides Dunal, *Sol. Syn.* 24. 1816. TYPE: Colombia. Fluvium Magdalenae, (holotype, P, = IDC microfiche 4375).

Solanum pseudolycioides Rusby, *Bull. Torrey Bot. Club* 26: 193. 1899. SYNTYPES: Bolivia. La Paz, 10,000 ft., *Rusby 833*; 12,000 ft., *Rusby 835* (both NY neither seen); *Bang 32* (NY not seen).

Solanum lyciiforme Dammer, *Engl. Jahrb.* 37: 168. 1905.

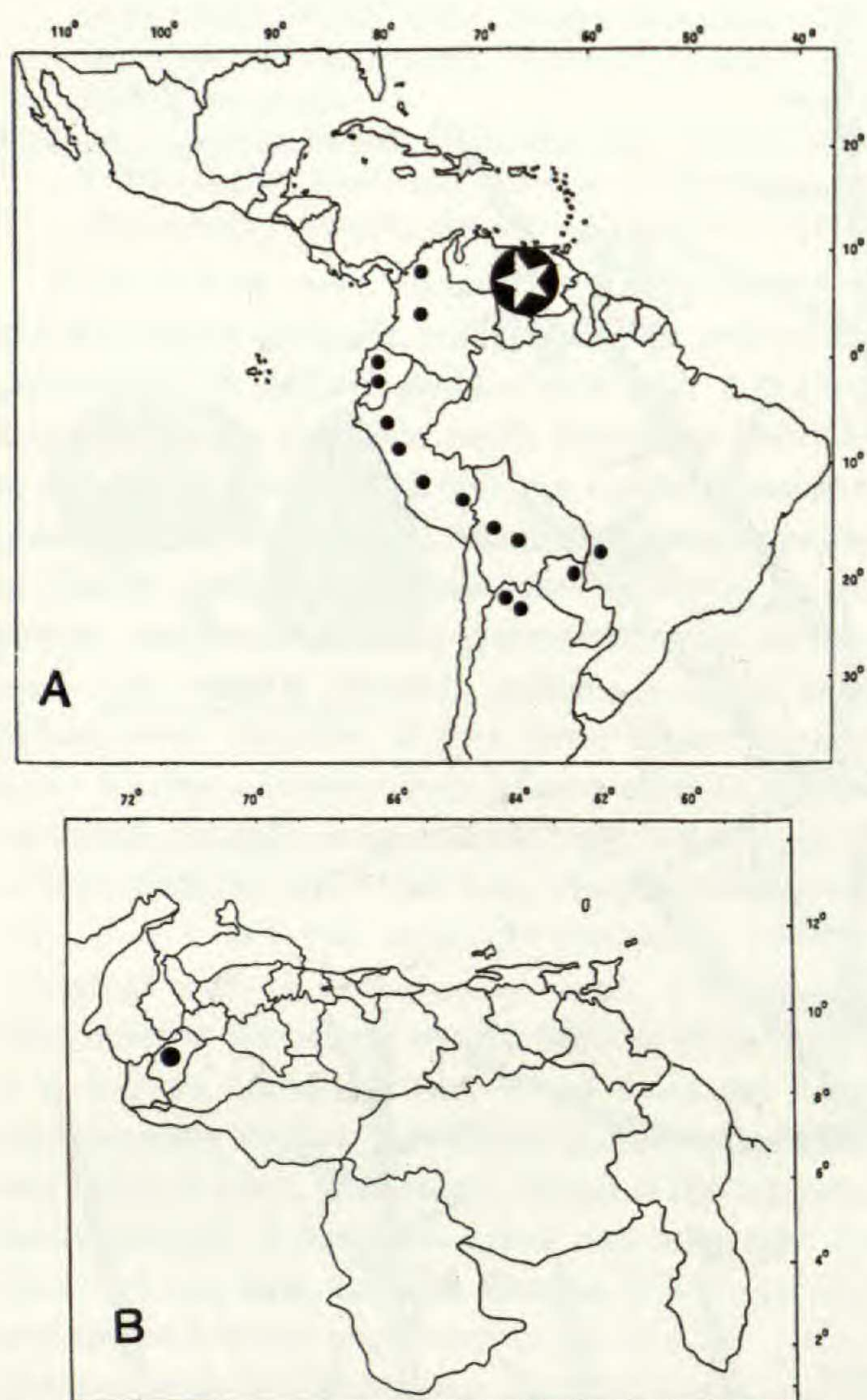


Figure 16. *Lycianthes lycioides*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

SYNTYPES: Argentina. Jujuy: Santa Catalina, *Claren* 11550; Yavi, *Fries* 985 (B not seen, CORD not seen). [Synonymy of Bitter, 1919 [1920]; Morton et al., 1976: 33; Barboza & Hunziker, 1992.]

Erect shrubs 0.5–1 m tall, much branched, young branches green, tomentose, adult branches strongly lignified, grayish, glabrescent, conspicuously lined, the shoots sometimes becoming spinose; pubescence of erect, sparingly branched hairs. Leaves solitary, often with short internodes and appearing dense or even fasciculate, elliptical, smaller leaves sometimes obovate, $0.6\text{--}2.5 \times 0.3\text{--}1.1$ cm, membranous or papery, both sides densely fine-pubescent, glabrescent, remaining apically tufted, veins 3–5 on each side, slightly elevated; petioles 2–4 mm long. Inflorescences fascicles of 3 or fewer flowers. Flowers diurnal, showy; pedicels 0.5–1.6 cm long; calyx $2\text{--}3 \times 0.3\text{--}0.5$ mm, pubescent to glabrate, teeth 10 in 2 unequal series, the upper series 1 mm long, the lower teeth 0.5 mm long, erect; corolla blue-violet with a yellow eye, rotate, the margin almost entire, the lobes strongly contrasting,

$1 \times 2\text{--}2.5$ cm, mostly glabrate; stamens unequal, 3 filaments 1.5–2.5 mm long, 2 filaments smaller, 0.5–1.2 mm long; anthers yellow to orange, 1.8–2.7 mm long; ovary ovoid, $1\text{--}2 \times 1\text{--}1.2$ mm, style 4–5 mm long, exerted 1 mm and curved, stigma bilobate. Berry orange, depressed-globose, 2–6 mm across, with 7–8 stone cells (pyrenes); fruiting calyx hardly accrescent, applied to the berry, the teeth spreading; fruiting pedicels slender, 8–20 mm long; seeds 1–2 per pyrene, each enclosed in sclerenchyma in the form of a pyrene. Figures 1E, 2B, 15; Jacquin, *Icones Plantarum Rariorum* 1, t. 46 (as *Solanum lycioides*); Ruiz & Pavon, *Fl. peruv.* 2: t. 177 (as *Solanum lycioides*); Edward's *Bot. Register* 32, t. 25. 1846 (as *Solanum lycioides*); Weddel, *Chloris Andina* 2, t. 55 (as *Solanum lycioides*); Bol. Mus. Paraense Hist. Nat. 4: 603. 1905–1906 (flower, as *Solanum lycioides*). [J. J. Jacquin, 1782. *Icones Plantarum Rariorum*. 1: t. 46, cites Jacq. Misc. 3.]

Especie con ramas espinescentes y corolas de un azul-violáceo intenso contrastando con el amarillo ladrillo hasta anaranjado de las anteras, bayas deprimido-globosas con 6 pirenos. Su distribución geográfica corresponde exclusivamente al estado Mérida en elevaciones entre 1900 y 3000 m.

Common name. “Cuchuva de Perro.”

This species is distinct with its spinescent branches, irregular branching, and small leaves. The corollas are intense blue-violet with a contrasting yellow or brownish eye.

The filaments in our material of this species are not gibbous as recorded by Barboza and Hunziker (1992). *Solanum lycioides* subsp. *parvifolium* (Wedd.) Bitter and *Solanum pseudolycioides* Rusby were considered to be synonyms by Bitter, and we hesitantly consider them to be the taxonomically typical *Solanum lycioides*. Material we have seen has slender, flexuous branching, apparently reflecting young growth rather than a distinct taxon.

Distribution. Uplands of Colombia, Ecuador, Peru, Bolivia, northwestern Argentina, Paraguay, and southern Brazil; in Venezuela in the Andean region. Semi-arid woody formations and remnants, 1900–3000 m elevation. (Map, Fig. 16.) Almost all collections are in flower, and most were made from April to July.

Representative specimens examined. VENEZUELA. Mérida: between El Morro & Mérida, 2000–2400 m, *Badillo* 6584 (MY); Mucuchíes, 2500 m, *Davidse & Steyermark* 18168 (VEN); Quebrada SW of Mucuchíes, 2600 m, *Nee & Whalen* 17053 (VEN); Caserío El Vergel between Mucurubá & Mucuchíes, 2900 m, *Ruiz-Terán & López-Palacios* 12533 (MERF, MY).

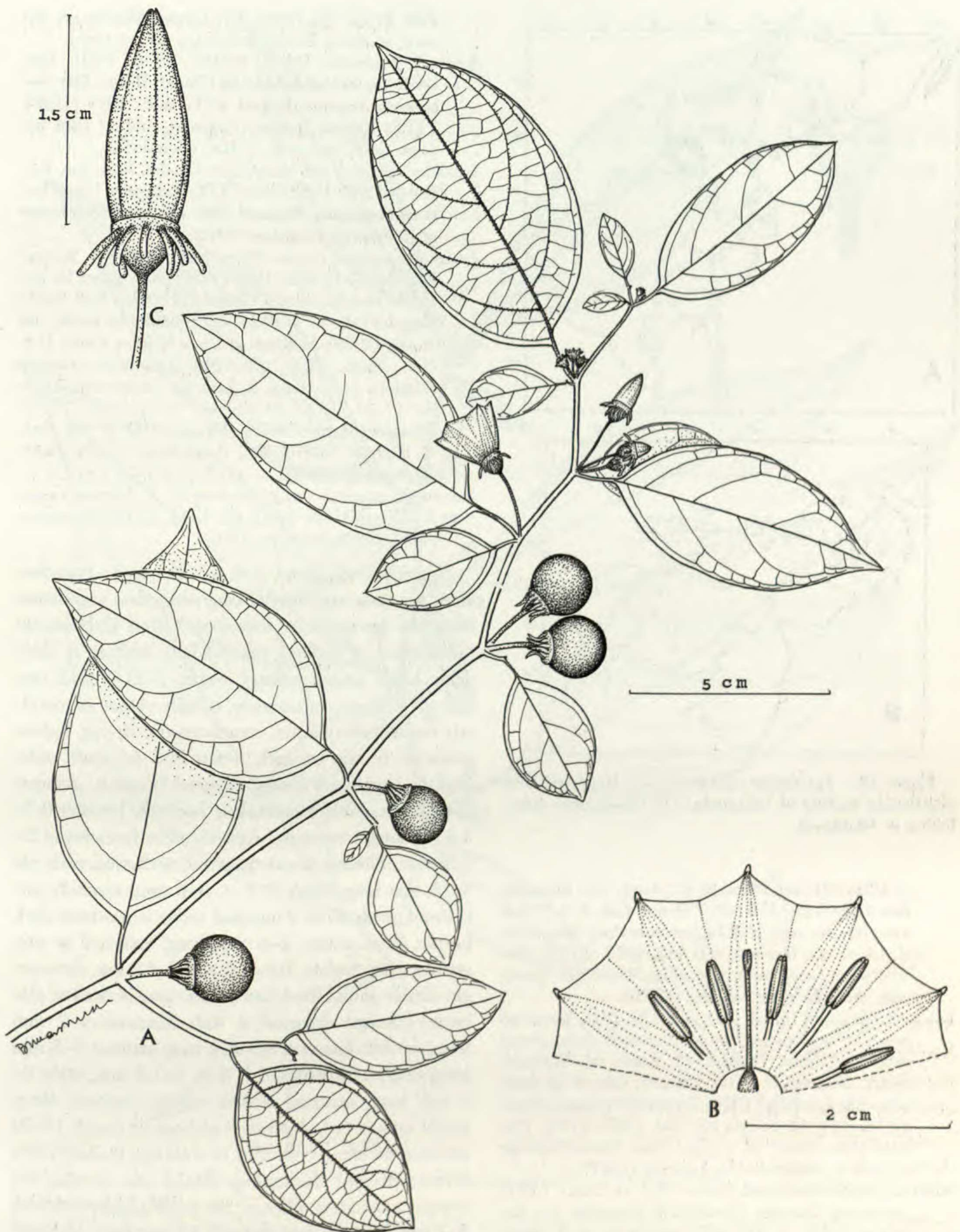


Figure 17. *Lycianthes pauciflora*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Flower bud. After Steyermark 123694 (MY) and Trujillo 13947 (MY).

8. *Lycianthes pauciflora* (Vahl) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 341. 1919 [1920]. Not Sendtn. (1846). *Solanum pauciflorum* Vahl, Eclog. Amer. 1: 20. 1796. TYPE: Martinique (holotype, C-hb Vahl).

Solanum geminatum Vahl, Eclog. Amer. 1: 21. 1797. *Lycianthes geminata* (Vahl) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 392. 1919 [1920]. TYPE: French Guiana. von Rohr s.n. (C, = F photo 22887). *Solanum neglectum* Dunal, Hist. Sol. 177. 1813. Based on *Solanum arborescens, solani hortensis folio, fructu*

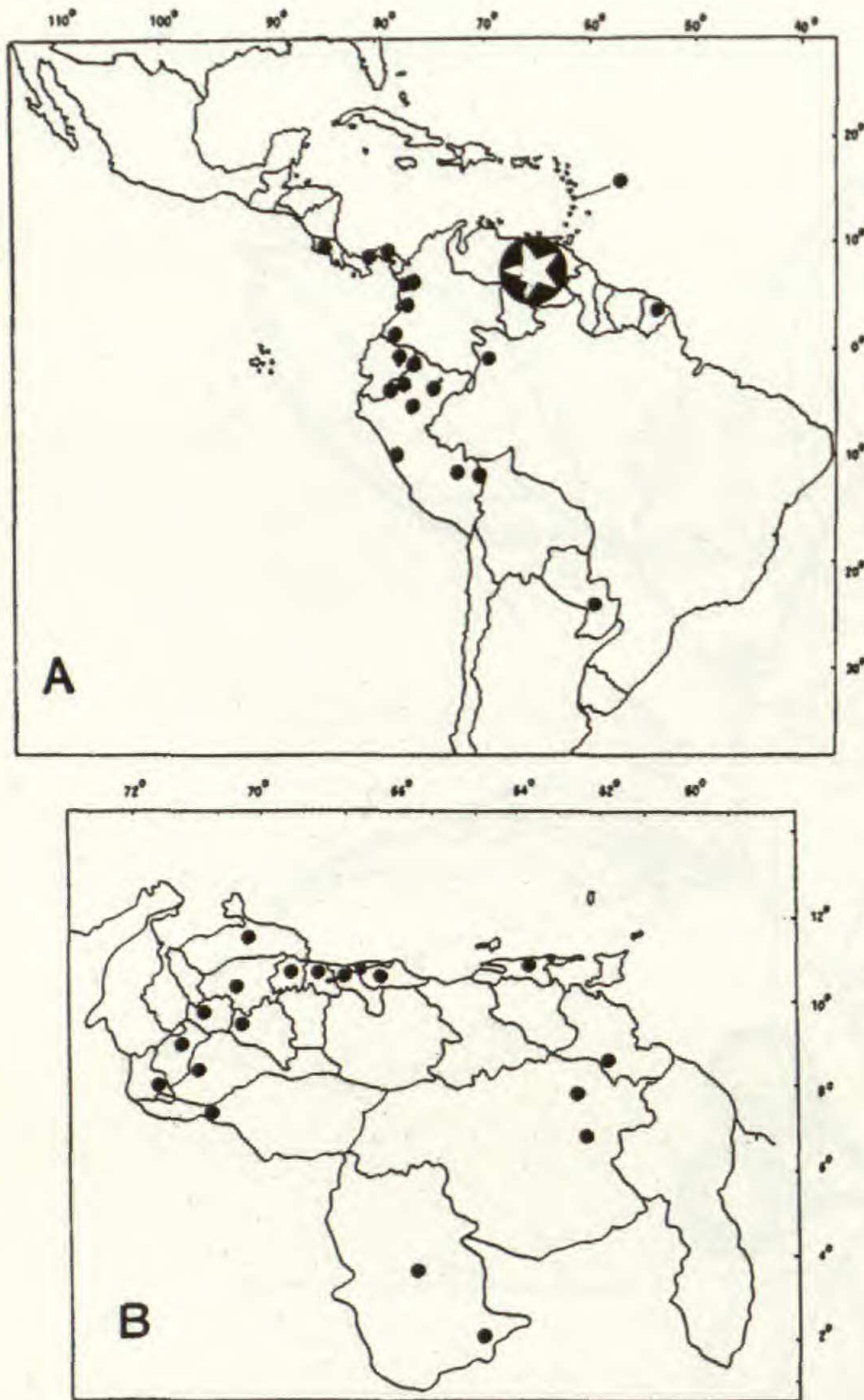


Figure 18. *Lycianthes pauciflora*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

corallino. *Maius*, Plumier, Pl. Amer. ed. Burmann 242, t. 245, fig. 4. 1760; Plumier, Cat. 4: 34 ined. mss., fide Lourteig (1987). *Lycianthes neglecta* (Dunal) Lourteig, Phytologia 62: 442. 1987. TYPE: Plumier plate based on a plant from Martinique (lectotype, designated by Lourteig (1987)).

Solanum speciosum Dunal, Hist. Sol. 179. 1813. Based on *Solanum arborescens, solani hortensis folio, fructu corallino*. *Minus*, Plumier, Pl. Amer. ed. Burmann 242, t. 245, fig. 5. 1760; Plumier, Cat. 4: 35 ined. mss., fide Lourteig (1987). *Lycianthes speciosa* (Dunal) Lourteig, Phytologia 62: 442. 1987. TYPE: Plumier plate based on a plant from Santo Domingo (lectotype, designated by Lourteig (1987)).

Solanum sylvaticum Dunal, Solan. Syn. 24. 1816. TYPE: Venezuela. Cumaná, *Humboldt & Bonpland, s.n.* (holotype, P-LA, = IDC 427 microfiche, = F photo, 39015).

Solanum glandulosum Sendtn., in Mart., Fl. Brazil 10: 52. 1846. SYNTYPES: Brazil. Amazonas: Rio Japura, *Martius s.n.* (B destroyed, M not extant, neither seen); southern Brazil, *Sellow* (B).

Solanum japurense Dunal, in DC., Prodr. 13(1): 174. 1852. New name for *Solanum glandulosum* Sendtn., in Mart., Fl. Brazil 10: 52. 1846, non Ruiz & Pavon (1799). *Lycianthes japurensis* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 350. 1919 [1920]. SYNTY-

PES: Brazil, Rio Negro, Rio Japurá, *Martius s.n.* not seen; southern Brazil, *Sellow s.n.* (B not seen).

Solanum guianense Dunal, in DC., Prodr. 13(1): 166. 1852. *Lycianthes guianensis* (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 346. 1919 [1920]. TYPE: French Guiana. Cayenne, *Aublet?* (BM not seen, G-DC not seen, = IDC microfiche).

Solanum urbanum var. *ovatifolium* Chodat, Bull. Soc. Bot. Genève 2(8): 152. 1916. TYPE: Paraguay. Grand forêt de Caaguazu, *Balansa 2080* not seen. [Synonymy of Barbosa & Hunziker (1992).]

Lycianthes pseudolycioides Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 352. 1919 [1920]. New name for *Solanum pseudolycioides* Chodat & Hassler, Bull. Herb. Boissier (ser. 2). 4: 84. 1904. Illegitimate name. Not Rusby (1899). *Solanum australe* Morton, Contr. U.S. Natl. Herb. 29(1): 63. 1944. *Lycianthes australe* (Morton) A. T. Hunz. & Barboza, Darwiniana 31(1-4): 17-34. 1992. Illegitimate combination. TYPE: Paraguay. Arroyo Moco, *Hassler 4912* (G not seen, = F photo, 23070, MO, P not seen, = US, photo, Morton neg. 8301).

Solanum caucaense var. *glabrescens* C. V. Morton, Contr. U.S. Natl. Herb. 29(1): 62. 1944. TYPE: Colombia. *Archer 2132* (holotype, US).

High-climbing *shrub* 5-6 m tall, upper branches often dangling and interlocking with other vegetation; branches ferruginous tomentose, often glabrescent; pubescence of stalked, pauciradiate stellate or dendritic hairs. *Leaves* solitary, ovate, 7-11 × 2-5 cm, apically obtuse or acuminate, basally obtuse or rounded, sometimes oblique, membranous, drying lighter green or brown beneath, veins 3-5 on each side, slightly impressed above, elevated beneath, glabrescent above, softly tomentulose beneath; petioles 0.7-1.6 cm long, tomentose. *Inflorescences* fascicles of 2-5 flowers. *Flowers* crepuscular and nocturnal; pedicels 7-16 mm long; calyx 2-7 × 3-6 mm, sparsely pubescent, teeth 10 in 2 unequal series, sometimes dark purple, later white, 2-6 mm long, reflexed or not; corolla white, rotate, 0.9-2.2 × 1.3-3.5 cm, the margin almost entire, the lobes conspicuously thicker, glabrate; stamens unequal, 4 with filaments 1-2 mm long, the fifth filament 3.3 mm long, anthers 2-5 mm long; ovary ellipsoidal, 1.5-2 × 1-1.5 mm, style 8-9 mm long, exerted 5 mm, stigma capitate. *Berry* bright orange-red, depressed globose or ovoid, 15-20 mm across, stone cells 2-3 or wanting; fruiting calyx accrescent and thickening, 10-14 mm across, the margin sometimes reflexed, the teeth usually reflexed, 3-7 mm long; fruiting pedicels 15 mm long, glabrate; seeds 40-80 per fruit, brown, 2.5-4 × 3.5-4 mm, the thickened margin ca. 0.7 mm wide. Figures 1A, B, D, 2G, 17; Plumier, Pl. Amer. t. 245, figs. 4, 5. 1760; D'Arcy, 1973: 640, fig. 13. [Plumier, Pl. Amer. ed. Burm. t. 245, fig. 4. 1760. as *Solanum peduncularis alaribus*.]

Es la especie de más amplia distribución geográfica en el país, muy variable en cuanto a grado de pubescencia,



Figure 19. *Lycianthes radiata*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Fruiting calyx. After Schwartzkoff 12 (MY).

siendo ésta densa y ferrugínea en las ramas jóvenes y floríferas y casi ausente en las ramas adultas y fructíferas, así mismo los dientes del cáliz varían en tamaño desde 2 hasta 6 mm de longitud, siendo reflejos o no en flor y/o en fruto, y el borde puede presentarse reflejo o aplicado; la corola presenta medidas entre 0.9–2.2 cm de longitud y el borde casi entero. Respecto a células pétreas, éstas

pueden estar ausentes o en número de 1, 2 ó 4, localizadas en la parte apical interior del fruto.

Common name. “Coronilla.”

This species is often seen climbing high in shrubs or low in the canopy and displaying large clusters of showy red fruits. The flowers, usually

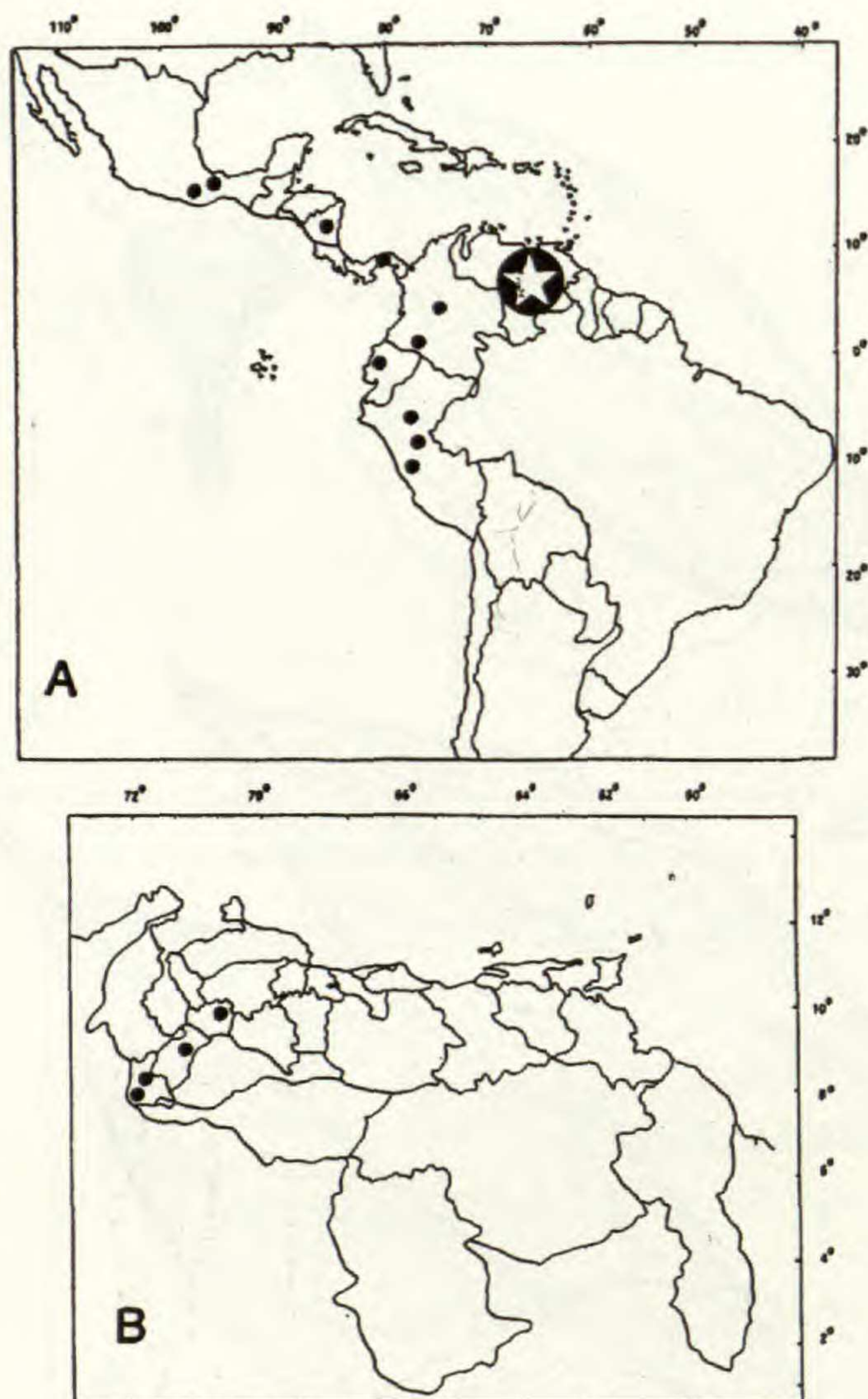


Figure 20. *Lycianthes radiata*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

closed during the day, are less conspicuous. The calyx has conspicuous, porrect, recurved or reflexed, sometimes almost woody teeth.

Distribution. Collections have been seen from Costa Rica, Panama, the Greater and Lesser Antilles, and all tropical countries in South America except Chile and the Guianas, and it probably occurs in the latter region. *Lycianthes pauciflora* is the most wide-ranging species of the genus within Venezuela, and it is variable as to its degree of pubescence and the size and form of its calyx teeth. Cloud forests and gallery forests 600–1500 m elevation. (Map, Fig. 18.) The species appears to flower and fruit throughout the year, but most flowering specimens were collected from April to July and in November and December.

The concept employed here unites concepts of several regional treatments (D'Arcy, 1973; Barboza & Hunziker, 1992) under the oldest name for this wide-ranging species. The Panamanian plants for which D'Arcy used the name *L. guianensis* Dunal have larger fruits and longer, thinner calyx lobes than those

from the Antilles, Venezuela, and other eastern parts of the continent, and they may represent a distinct taxon. However, in most particulars, particularly in having fruits with 2 stone cells, the Venezuelan plants agree with the other plants discussed here. Plants of the species from the Antilles, particularly Dominica and Martinique, the type locality of *L. pauciflora*, tend to have slightly smaller calyces and flowers and more rotund leaves than those of Venezuela and the Guianas, but they are otherwise similar. Fruits examined from the Lesser Antilles had varying numbers of stone cells (Martinique, *Duss* 364 (US), no stone cells, *Duss* 4430 (US), 1 stone cell, Dominica, *Ernst* 1942 (US), 2 stone cells). Plants from lowland Paraguay, Bolivia, and Peru have dimensions like those of plants from the Antilles.

Representative specimens examined. VENEZUELA. **Distrito Federal:** between el topo Macanillal & El Pico Izcaragua, 7–12 km E de los tanques de la Electricidad de Caracas, 700–800 m, *Morillo et al.* 3272 (VEN). **Amauro:** Reserva forestal Sierra Imataca, 1988 m, *Sanoja* 2002 (MY). **Amazonas:** 5 to 7 km by river E of Cerro La Neblina, 140 m, *Liesner & Funk* 15838 (MO, MY, VEN). **Apure:** Reserva Forestal de San Camilo, Chiricoa, 200 m, *Steyermark et al.* 101704 (MO, NY). **Aragua:** Carretera Maracay–Choroní, 1200 m, *Benítez et al.* 4911 (MY). **Barinas:** Dist. Bolívar, near feldspar mine, between La Soledad and Santo Domingo, 1300 m, *van der Werff & Ortega* 6124 (MO, NY). **Bolívar:** El Dorado-La Gran Sabana, 1200 m, *Bunting* 2908 (MY). **Carabobo:** Colinas de Guaremales, en la Fortaleza, *Pittier* 8803 (VEN). **Falcón:** Sierra de San Luis, S of La Tabla, 1450 m, *Steyermark* 98911 (MO). **Lara:** above Sanare toward Las Blancitas, 1500–1900 m, *Badillo* 6687 (MY). **Mérida:** Carretera Estanquez–Las Nieves, 850 m, *Benítez et al.* 4826 (MY). **Miranda:** Parque Nacional Guatopo. La Macanilla, 600 m, *Nee* 17760 (MO, NY). **Portuguesa:** E of Chabasquen, 1450–1520 m, *Steyermark et al.* 126813 (VEN). **Sucre:** Cerro Patao, N of Puerto de Hierro, *Steyermark & Agostini* 91324 (VEN). **Táchira:** between Quebrada Grande and El Nula, border with Apure, 250 m, *Gentry & Puig-Ross* 14293 (MO). **Trujillo:** Vía Escuque-El Socorro, *Benítez* 1952 (MY). **Yaracuy:** Serranía Santa María-Cerro La Chapa, 6 km N de Nirgua, 1200–1350 m, *Meier et al.* 3903 (MY, VEN).

9. *Lycianthes radiata* (Sendtn.) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 433. 1919 [1920]. *Solanum radiatum* Sendtn., in Martius, Fl. Brazil. 10: 53. 1846. TYPE: *Hartweg* 1293 [129 in publication] (BREM not seen, W not seen, B destroyed, = F photo 2586).

Solanum goudoti Dunal, in DC., Prodr 13(1): 158. 1852. *Lycianthes goudoti* (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 435. 1919 [1920]. TYPE: Colombia. *Goudot* 13 (holotype, G-DC not seen, = IDC microfiche, = F photo, 006772, W not seen).

Lycianthes holocalyx Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 459. 1919 [1920]. TYPE: Ecuador. Provincia Santo Domingo, *Sodirol* 114/38 (B destroyed, = F photo 2577)

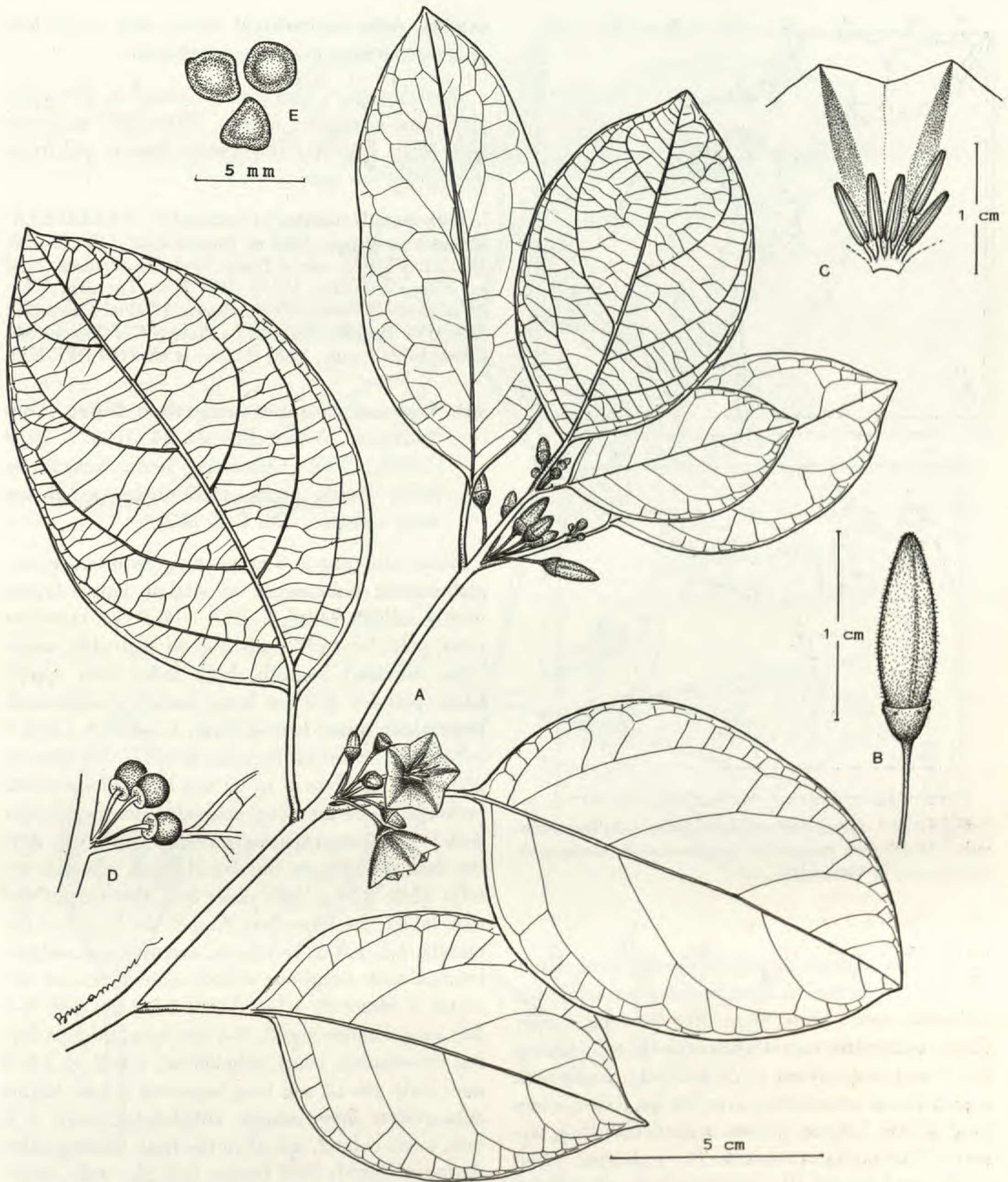


Figure 21. *Lycianthes sanctaemarthae*.—A. Flowering branch.—B. Flower bud.—C. Opened flower.—D. Infructescence.—E. Seeds. A, B, C. After Steyermark et al. 122959 (VEN); D, E. After Bunting 10185 (MO).

Erect or wandlike *shrub* 1–2 m tall, young stems densely pubescent, sometimes glabrescent; pubescence of weak, simple, ascending hairs, those on the internodes to 5.5 mm long. *Leaves* unequal-geminate, major leaves elliptical, sometimes oblique, basally obtuse, the reduced side cuneate, apically acuminate, 10–19 × 3–7 cm, membranous, paler beneath, pilose on both sides, more so

beneath, sometimes glabrescent above, veins 7–9 on each side, elevated beneath; minor leaves decurrent on the petiole, 5–9 × 2–3 cm; petioles 0.8–2 cm long, plane above. *Inflorescence* 5–16-flowered. *Flowers* diurnal, a few opening at a time; pedicels 0.6–1.8 cm long, slender, dispersed or densely pubescent with ascending hairs; calyx 2–3.2 mm long and wide, densely pubescent outside,

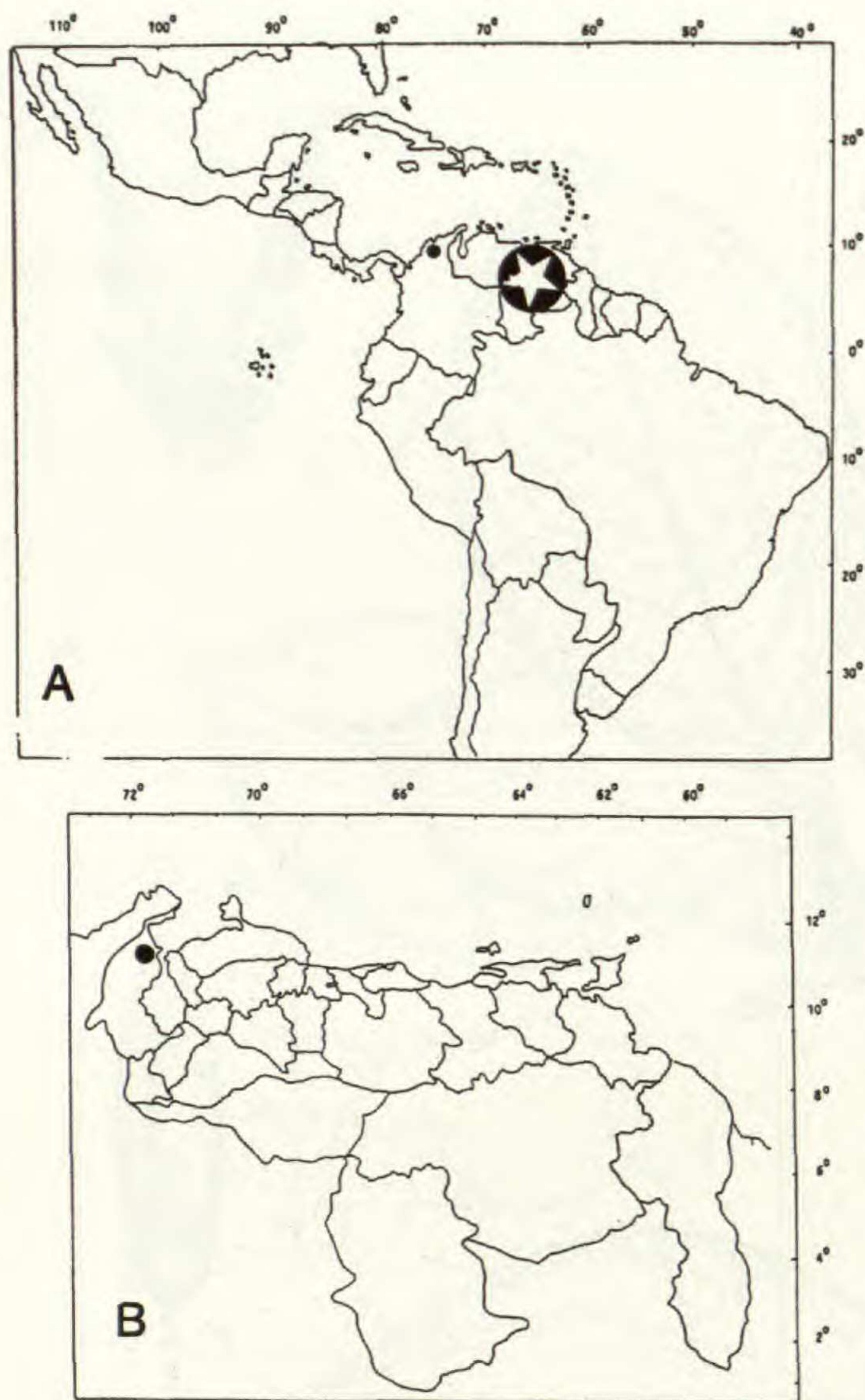


Figure 22. *Lycianthes sanctaemarthae*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

inside with minute, dispersed glands, teeth wanting, the 10 nerves evident, sometimes somewhat elevated; corolla white, rotate, 6–8 mm long, deeply lobed, puberulent outside; stamens equal, filaments 2–2.9 mm long, anthers 2–2.5 mm long, drying with a dark dorsal connective; ovary ovoid, 1.2–1.5 mm long \times 0.8–1.3 mm across, style 6 mm long, exerted 3 mm, stigma capitate. *Berry* globose, 5.5–8 mm across, stone cells absent; fruiting calyx slightly accrescent, 2 mm long, mostly strigose; seeds 50–70 per fruit, dark brown, 0.5–1 \times 0.75–1.5 mm. Figures 2K, 19.

Esta especie es la única dentro de la Sección *Simplicipila* en Venezuela que no presenta dientes en el cáliz, mostrando 10 nervios conspicuos y un tanto elevados.

This is the only species in section *Simplicipila* in Venezuela that has no teeth on the calyx.

The foliage and pubescence of this species is extremely variable, and the material cited may represent more than one taxon. *Dorr et al.* 5104 has

smaller, more symmetrical leaves with much less pubescence than the other specimens.

Distribution. Venezuela, Colombia, Ecuador, and Peru. Evergreen forests, 1900–2800 m elevation. (Map, Fig. 20.) The species flowers and fruits throughout the year.

Representative specimens examined. VENEZUELA. **Mérida:** La Mucuy, 1900 m, *Benítez et al.* 4185 (F, MO, MY, NY, VEN); E side of Prado Verde-Las Cuadras, 2150 m, *D'Arcy & Benítez* 18257 (MO, MY). **Táchira:** 1 km SE of alcabala Páramo El Zumbador, 2750 m, *Pietrangeli* 388 (MY). **Trujillo:** between La Playa SW of Carache and Potreritos de Cendé, 2200 m, *Dorr et al.* 5104 (MY, NY).

10. *Lycianthes sanctaemarthae* Bitter, Abh. Naturwiss. Vereine Bremen 24 (1): 377. 1919 [1920]. TYPE: Colombia. Sierra Nevada de Santa Marta, *Smith* 1189 (holotype, B not seen; isotypes, CM, F-2, MO).

Shrub climbing to 8 m, young growth tomentose, glabrescent; pubescence of stellate hairs. *Leaves* mostly solitary, ovate, 8–10.5 \times 4–8 cm, membranous, paler beneath, veins 3–5 on each side, major veins elevated beneath, both sides with sparse hairs; petioles 1–3 cm long, basally compressed, puberulent; minor leaves ovate, 1.5–2.8 \times 1.5–2.5 cm. *Inflorescences* in fascicles of 6–13(–16) flowers; peduncles obsolete or to 10 mm long. *Flowers* with pedicels 11–14 mm long, sparsely pubescent; calyx 3–3.5 \times 4–5 mm, sparingly evenly pubescent, drying dark, the margin translucent, teeth wanting; corolla white with a light violet line, the margin sinuate-lobed, the lobes less than $\frac{1}{3}$ the length of the corolla, 1.1–1.8 \times 2–3.5 cm, evenly dispersed pubescent with simple or stellate hairs; stamens unequal, 4 filaments 1.5–2.2 mm long, the fifth 4–5 mm long, anthers equal, 5–6 mm long, the tips drying discolourous; ovary subglobose, 1.5–2 \times 1.5–3 mm, style 10–12 mm long, exerted 2 mm, stigma subcapitate. *Berry* orange, subglobose, 9–12 \times 8 mm, stone cells 2, apical in the fruit; fruiting calyx drying uniformly dark brown, 6–8 mm wide, sometimes developing umbos on the sides; fruiting pedicels to 2 cm long; seeds ca. 55 per fruit, yellowish brown, 2–2.5 mm, the thickened margin ca. 0.5 mm wide. Figures 2D, 21.

Presenta el cáliz edentado y la pubescencia está representada por tricomas estrellados. Los frutos presentan células pétreas, a diferencia de lo señalado en la literatura en donde en la Sección *Virgatae* a la que pertenece ésta especie, no se mencionan células pétreas.

The calyx of this species lacks teeth and the pubescence is stellate.

Distribution. Restricted to the Sierra Nevada

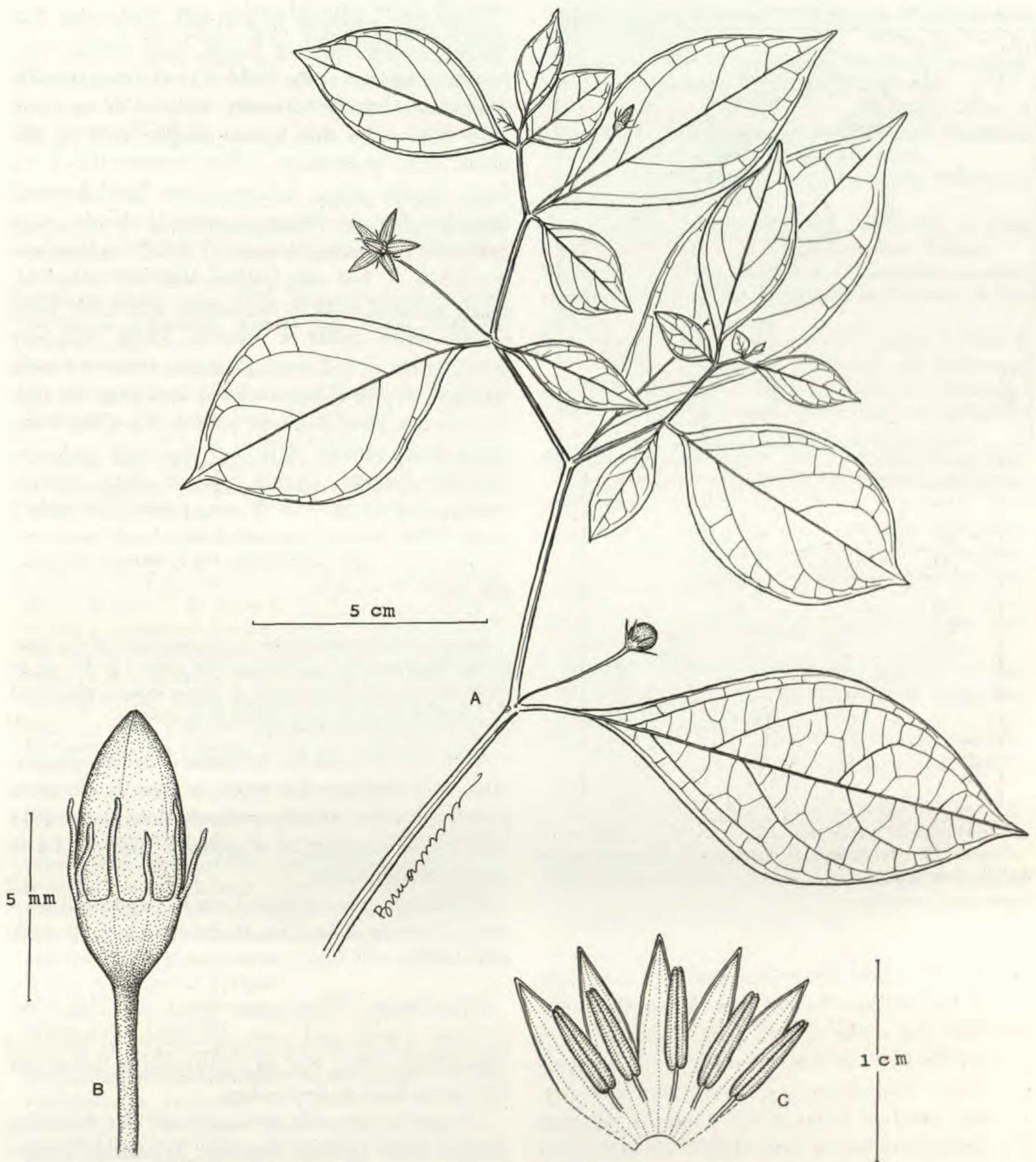


Figure 23. *Lycianthes stenoloba*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower. After Mocquerys 978 (MY).

de Santa Marta in Colombia and in the Río Guasare watershed in Zulia State in Venezuela. Riverine forests from 500 to 600 m elevation. (Map, Fig. 22.) We have seen flowering specimens from May and June and fruiting specimens from August.

Although Bitter reported an absence of stone cells in the fruits of this species, we found two in the fruit we examined (Bunting & Kauffman 10257).

Representative specimens examined. VENEZUELA.

Zulia: Dist. Mara, Cuenca de los ríos Socuy-Guasare, en la Paloma, 600 m, *Bunting 10185* (MO), *Bunting & Kauffman 10257* (MO); E of río Guasare, 600 m, *Steyermark et al. 122959* (NY, VEN); Cerro Los Manantiales, E of río Guasare, W of Hacienda Los Manantiales, 600 m, *Steyermark et al. 123281* (NY, VEN).

11. *Lycianthes stenoloba* (van Heurck & Muell.-Arg.) Bitter, *Abh. Naturwiss. Vereine Bremen* 24(1): 358. 1919 [1920]. *Solanum stenolobum* van Heurck & Muell.-Arg., *Observ.*

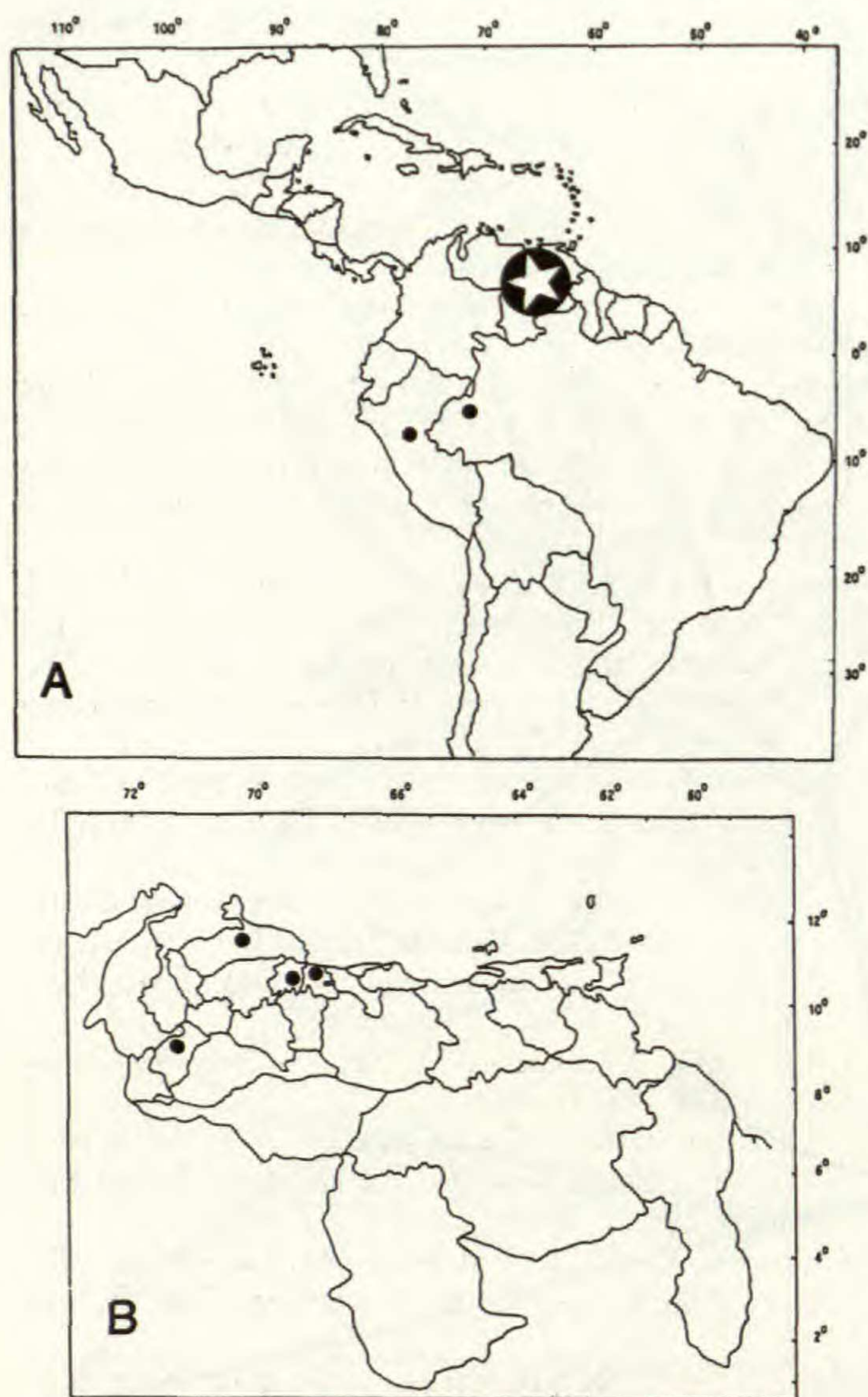


Figure 24. *Lycianthes stenoloba*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Bot. 69. 1870. *Bassovia stenoloba* (van Heurck & Muell.-Arg.) Britton, Mem. Torrey Bot. Club 4(3): 232. 1895. TYPE: Peru. Prope Tarapoto, Spruce 4210 (G-DC not seen, = IDC microfiche). [A duplicate (syntype) of this collection was cited as being in van Heurck's personal herbarium, but its whereabouts are unknown.]

Lycianthes acutangula Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 357. 1919 [1920]. *Solanum acutangulum* (Bitter) MacBride, Field Mus. Nat. Hist. 13(V-B) 1: 229. 1962. TYPE: Peru. San Govan, Lechler 2354 (holotype, G, = F photo 23064).

Solanum compressibaccatum (Bitter) Bitter, Repert. Spec. Nov. Regni Veg. 12: 456. 1913. *Lycianthes acutangula* subsp. *compressibaccata* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 358. 1919 [1920]. TYPE: Peru. Ule 6800 (B not seen, = F photo 2560 MO, MY).

Lycianthes longidentata Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 356. 1919 [1920]. *Solanum longidentatum* (Bitter) C. V. Morton, Contr. U.S. Natl. Herb. 29(1): 64. 1944. TYPE: Brazil. Rio Acre, Estella, Seringal, S. Francisco, Ule 9733 (holotype, B destroyed, = F photo 2582; isotype, US).

Sprawling *subshrub* to 4 m tall, internodes 3–6 cm long; pubescence of simple hairs. *Leaves* solitary or geminate, ovate, 9–14 × 3–6.5 cm, apically acuminate, basally cuneate, veins 4–6 on each side, both sides with sparse simple hairs on the main veins, glabrescent, ciliate; petiole 0.5–2 cm long, slightly pilose. Inflorescences 1(–4)-flowered fascicles. Flowers ?diurnal; pedicels slender, very gradually expanding upwards, 1.5–4.5 cm long; calyx 2.5–3 × 1–3 mm, pilose, with 10 subapical, erect, unequal teeth in one series, 2.5–5 mm long; corolla white, rotate or reflexed, lobed ½–⅓ way down, 1–1.5 × 1–2.5 cm, glabrous; stamens mostly unequal, 4 with filaments 0.2–1 mm long, the fifth 0.1–2.5 mm long, glabrous, anthers 4.5–6 mm long; ovary ovoid-conical, style 5–8 mm long, glabrous, exerted 1.5 mm, stigma bilobed. Berry orange, compressed-ovoid, 9 × 8 mm, sometimes with 2 stone cells; fruiting calyx 8.5 mm long; seeds ca. 24 per fruit, yellowish brown, 3 × 2 mm. Figures 2H, 23.

Esta especie es conspicua por la longitud de sus pedicelos florales cuyas medidas oscilan entre 1.5–4.5 cm de longitud y la corola presenta el borde lobado, con lobos de longitud ½–⅓ de la longitud de la corola.

This species can be recognized by its slender, often wide-flaring calyx teeth, its usually elongate, slender usually arching pedicels, and its anthers held tightly together in a cylinder. The corolla is conspicuously lobed.

"*Solanum acutangulum* Griseb." appeared as a nomen nudum in Lechler, Berberid. Amer. Austral. (58. 1857).

Distribution. Venezuela, Brazil, and Peru. Deciduous woods and semi-deciduous riversides, 200–700 m. (Map, Fig. 24.) Collected in flower and fruit from June to September.

Lycianthes stenoloba is much like the following species from Central America: *Lycianthes guatemalense* Bitter, *Lycianthes stephanocalyx*, (J. S. Brandeg.) Bitter, and *Lycianthes solitarium* (Blake) Standl. The Central American species were treated in part by Gentry and Standley (1974) and Dean (1995), and Nee (1986) treated *Lycianthes stephanocalyx* for Veracruz, Mexico. The name *L. stenoloba* is employed for this species with hesitation. In the original description and in the type photos and other material seen for the synonyms cited, the calyx is mostly longer—4–9 mm as opposed to 2–3 mm—than in the Venezuelan material. Bitter reported finding two stone cells in fruits of this species, but we found none in the fruits we examined.

Representative specimens examined. VENEZUELA.

Carabobo: Valle Seco, camino hacia La Toma, 100–200 m, Benítez & Pons 4654 (MY). **Falcón:** Sierra de San Luis, between Santa Lucía and Cabure, 800 m, van der Werff & B. Vera 864 (CORO, MY). **Mérida:** El Vigía, Macqueys 978 (MY, P). **Yaracuy:** Finca Antonia, San Felipe, Ferrari 791 (MY).

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LIST OF SPECIES

1. *Lycianthes acutifolia* (Ruiz & Pavon) Bitter
2. *Lycianthes amatitlanensis* (Coult. & J. D. Smith) Bitter
3. *Lycianthes asarifolia* (Kunth & Bouché) Bitter
4. *Lycianthes ferruginea* Bitter
5. *Lycianthes inaequilatera* (Rusby) Bitter
6. *Lycianthes lenta* (Cav.) Bitter
7. *Lycianthes lycioides* (L.) Hassler
8. *Lycianthes pauciflora* (Vahl) Bitter
9. *Lycianthes radiata* (Sendtner) Bitter
10. *Lycianthes sanctaemarthae* Bitter
11. *Lycianthes stenoloba* (van Heurck & Muell.-Arg.) Bitter

COLLECTIONS OF LYCIANTHES FROM VENEZUELA STUDIED

Specimens are listed alphabetically by collector, followed by collector number and herbarium of deposit; the species is indicated by a number in parentheses corresponding to the number in the text and in the List of Species.

Adamo s.n. (MERC) (7). Agostini 3 (VEN) (8). Agostini et al. 1701 (VEN) (11). Allart 318-2 (NY, VEN) (1). Aristeguieta 1749 (NY, VEN) (8); 3994 (MO, VEN) (6); 4233 (MO, NY, VEN) (1); 7122 (NY) (1). Aristeguieta & Foldats 1406 (VEN) (3). Aristeguieta & Pannier 1973 (VEN) (3).

Aymard & Flores 216 (MY, PORT, VEN) (7). Aymard et al. 1643 (MY, PORT) (8); 2839 (MY, PORT) (3).

Badillo 1816 (MY) (6); 1914 (MY) (8); 4426 (MY) (8); 5672 (MY) (4); 6584 (MY) (7); 6636 (MY) (8); 6687 (MY) (4). Badillo & Holmquist 6217 (MY) (8). Badillo et al. 7841 (MY) (8). Benítez 318 (MY) (6); 517 (MY) (3); 683 (MY) (7); 1181 (MY) (8); 1335 (MY) (8); 1353 (MY) (8); 1408 (MY) (4); 1418 (MY) (1); 1446 (MY) (4); 1551 (MY) (1); 1554 (MY) (6); 1562 (MY) (8); 1952 (MY) (8); 2068 (MY) (4); 2243 (MY) (8); 2614 (MY) (6); 3214 (MY) (6); 3621 (MY, NY) (3); 3868 (MY) (1); 3869 (MY) (4); 3898 (MY) (1). Benítez & Otero 4609 (MY) (1). Benítez & Pons 4651 (MY) (3); 4654 (MY) (11). Benítez & Rojas 3087 (MY) (8); 3993 (MY) (3); 5000 (MY) (8). Benítez et al. 3221 (MY) (3); 4184 (MY) (7); 4185 (F, MO, MY, NY, VEN) (9); 4235 (MY) (4); 4236 (MY) (1); 4259 (MY) (3); 4261 (MY) (8); 4611 (MY) (9); 4847 (MY) (9); 4884 (MY) (8); 4911 (MY) (8); 5104 (MY) (4); 5117 (MY) (4); 5129 (MY) (4); 5148 (MY) (4). Bernardi 433 (MER) (1); 1834 (VEN) (1); 2327 (NY, MER) (8); 5687 (NY) (8); 5792 (MER, NY) (3); 5930 (MER) (8). Berry 940 (VEN) (4); 944 (VEN) (1). Bianco 39 (CAR, VEN) (3); Bianca 302 (MER, MO, VEN) (8). Bonpland 71 (P) (6). Breteler 3628 (MER, VEN) (1). Bunting 2908 (MY) (8); 3020 (MY) (8); 4433 (MY) (6); 5808 (VZU, MO, VEN) (6). Bunting 10185 (MO) (10). Bunting & Kauffmann 10257 (MO) (10); Burkart 16324 (VEN) (6).

Cárdenas 4038 (MY) (8). Castillo 1930 (MY) (9). Carnevali et al. 614 (MY, VEN) (8). Cesari (VEN-249120) (1). Colonello 930 (CAR) (8). Croat 54841 (VEN) (5). Cumana 1850 (IRBR, MY) (6).

D'Arcy & Benítez 18257 (MO, MY) (9). Davidse 4035 (VEN) (4). Davidse & Steyermark 18168 (VEN) (7). Davidse & González 18899 (NY, VEN) (5); 21914 (NY) (8). Davidse & Miller 27476 (MO, MY) (8). Delascio 51 (CAR) (3); 122 (CAR) (1); 981 (CAR) (4); 9026 (CAR) (4). Delascio & de Delascio 2692 (CAR, VEN) (3). Delascio & López 12838 (MO, VEN) (3). Demey (CORO, MY-86695) (4). Diederichs 173 (VEN) (4); 177 (VEN) (8); 270 (VEN) (8); 279 (VEN) (8). Dorr & Barnett 7183 (MER, MO) (8). Dorr et al. 4749 (MY, NY) (8); 5104 (NY, VEN) (9); 5263 (NY) (7). Duno et al. 184 (MY) (6).

Edwards et al. 94 (MY) (8).

Fendler 974 (MO, P) (1); 991 (G, MO, NY) (4); 1065 (NY) (3). Fernández, A. 379 (MY) (3); 497 (MY) (6); 606 (MY) (8); 620 (MY) (8); 1112 (MY) (8); 3697 (MY) (1); 3762 (MY) (8); 3963 (MY) (8); Fernández, F. 98 (VEN) (8). Ferrari 733 (MY) (8); 790 (MY) (3); 791 (MY) (11); 859 (MY) (7).

Gentry & Puig-Ross 14293 (MO) (8). Gentry & Stein 47275 (MO, MY, VEN) (8).

Humbert 26108 (MER, P) (1); 26156 (MER, P) (1). Humboldt 748 (P) (6).

Ijjasz & Madriz 164 (MY, VEN) (7).

Jahn 1211 (VEN) (6); 1248 (VEN) (6). Jeffrey & Trujillo 2510 (MY) (8).

Knapp & Mallet 6766 (BH, MY) (2); 6807 (BH, MY, VEN) (1).

Lasser 1068 (VEN) (4); 1203 (VEN) (4); 2044 (VEN) (8); 2212 (VEN) (8). Licata et al. 32 (MY, PORT) (3). Liesner 10038 (VEN) (1); 12833 (MY, VEN) (5). Liesner & Funk 15838 (MO, MY, VEN) (8). Liesner & González 9732 (VEN) (8); 9773 (VEN) (2); 9969 (VEN) (8). Liesner & Guariglia 11631 (MO, NY, VEN) (8). Liesner et al. 7803 (MY, MO, VEN) (3). Linden 437 (G) (4); 478 (P) (3). López-Figueiras & Rodríguez 9080 (MERF) (7). López-Palacios 1457 (MERF, MO, MY) (7); 1539 (MO) (4); 2206

(MERF, MY, VEN) (8). López-Palacios & Bautista 3485 (MER) (8).

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